Article

Effects of moisture and density-dependent interactions on tropical tree diversity

https://doi.org/10.1038/s41586-023-05717-1

Received: 22 October 2020

Accepted: 8 January 2023

Edwin Lebrija-Trejos[1]✉, Andrés Hernández[2] & S. Joseph Wright[2]

Tropical tree diversity increases with rainfall[1,2]. Direct physiological effects of moisture availability and indirect effects mediated by biotic interactions are hypothesized to contribute to this pantropical increase in diversity with rainfall[2–6]. Previous studies have demonstrated direct physiological effects of variation in moisture availability on tree survival and diversity[5,7–10], but the indirect effects of variation in moisture availability on diversity mediated by biotic interactions have not been shown[11]. Here we evaluate the relationships between interannual variation in moisture availability, the strength of density-dependent interactions, and seedling diversity in central Panama. Diversity increased with soil moisture over the first year of life across 20 annual cohorts. These first-year changes in diversity persisted for at least 15 years. Differential survival of moisture-sensitive species did not contribute to the observed changes in diversity. Rather, negative density-dependent interactions among conspecifics were stronger and increased diversity in wetter years. This suggests that moisture availability enhances diversity indirectly through moisture-sensitive, density-dependent conspecific interactions. Pathogens and phytophagous insects mediate interactions among seedlings in tropical forests[12–18], and many of these plant enemies are themselves moisture-sensitive[19–27]. Changes in moisture availability caused by climate change and habitat degradation may alter these interactions and tropical tree diversity.

Direct effects of moisture availability on plants and their enemies are well known and are hypothesized to contribute to increases in plant diversity with moisture availability across the tropics[1–5]. Direct effects of moisture availability on plants range from adaptive physiological responses to seasonal water deficits, which contribute to tree species turnover along tropical rainfall gradients[7,8,28], to physiological failure under prolonged deficits during drought, which causes species-specific changes in mortality rates that alter the species composition of forests worldwide[5,7–10]. The physiological tolerance hypothesis proposes that these direct physiological effects of moisture on plants could increase plant diversity if more moisture-sensitive species were able to recruit and survive as moisture availability increased[5,10].

The direct effects of moisture availability on plant enemies might also have indirect effects on plant performance and diversity. As moisture availability increases, tropical phytophagous insects tend to increase their activity[19–23], and primary pathogenic fungi and oomycetes (water moulds) tend to increase their dispersal, growth and infection rates of healthy hosts[24,25]. The enemies hypothesis[3,4,6] proposes that phytophagous insects and microbial pathogens decrease the survival of their plant hosts in areas with high host density[12–16,29,30] and that this conspecific negative density dependence (CNDD) suppresses locally abundant species and advantages locally rare species, thereby contributing to plant diversity[14,30–32]. The direct effects of moisture availability on plant enemies could thus increase plant diversity if CNDD strengthened as moisture availability increased[11,26].

Here we evaluate the relationships between temporal variation in moisture availability, differential survival of moisture-sensitive species, the strength of CNDD, and plant diversity in a tropical moist forest. We then use simulations to explore how moisture-dependent variation in CNDD and species-specific survival affect diversity. We use a census of seedlings of 215 species for 20 years, including the driest and second wettest years since local rainfall records began in 1926 (Extended Data Fig. 1 and Methods). Diversity tended to decline over the first year of seedling life in drier years and to increase in wetter years (Fig. 1 and Extended Data Fig. 2a). We evaluated two mechanisms that might contribute to this relationship between diversity and moisture availability. First, moisture availability might increase the survival of moisture-sensitive species and thereby enhance diversity during wetter years. Second, moisture availability might strengthen CNDD and thereby suppress abundant species, advantage rare species and enhance diversity during wetter years. The two mechanisms are mutually compatible and both are hypothesized to enhance diversity with increases in moisture availability along geographical gradients[1–5,10].

We used generalized linear mixed models (GLMMs) to explore how first-year seedling survival varied with mean wet season soil moisture content (SM_w), species-specific moisture optima (SPMO) and the strength of conspecific density dependence (Methods). SPMO were determined from the distributions of 550 tree species across a twofold rainfall gradient extending from the dry Pacific to wet Caribbean coasts of central Panama[8] and are strongly related to species-specific drought

---

[1]Department of Biology and Environment, University of Haifa–Oranim, Kiryat Tiv'on, Israel. [2]Smithsonian Tropical Research Institute, Balboa Ancón, Panama. ✉e-mail: edwin-l@sci.haifa.ac.il

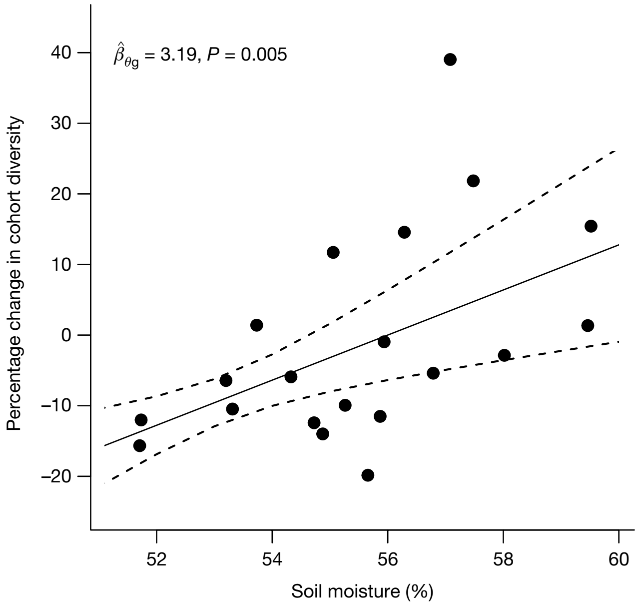


Fig. 1 | The relationship between soil moisture and changes in seedling diversity over the first year of seedling life for 20 seedling cohorts. The change in diversity tended to increase from negative values (decreasing diversity) in drier years to positive values (increasing diversity) in wetter years (Spearman correlation = 0.62, two-tailed AS89 algorithm, $P = 0.004$, $n = 20$). The black line depicts the mean response estimated with a generalized least-squares analysis that accounts for heterogeneity of variance. Dashed lines are the bootstrapped 95% confidence intervals around the mean response. Soil moisture is the mean gravimetric soil water content (θ_g) during the wet season. Diversity was quantified as the effective number of species or Hill number (^2D), the inverse of the Simpson dominance index, which places more weight on abundant than rare species. The pattern is qualitatively similar for ^1D, the exponential Shannon–Wiener diversity index, which weights species by their abundance without favouring common or rare species (Extended Data Fig. 2a). $\hat{\beta}_{\theta_g}$ is the slope of the fitted model (P value based on a two-tailed t-test).

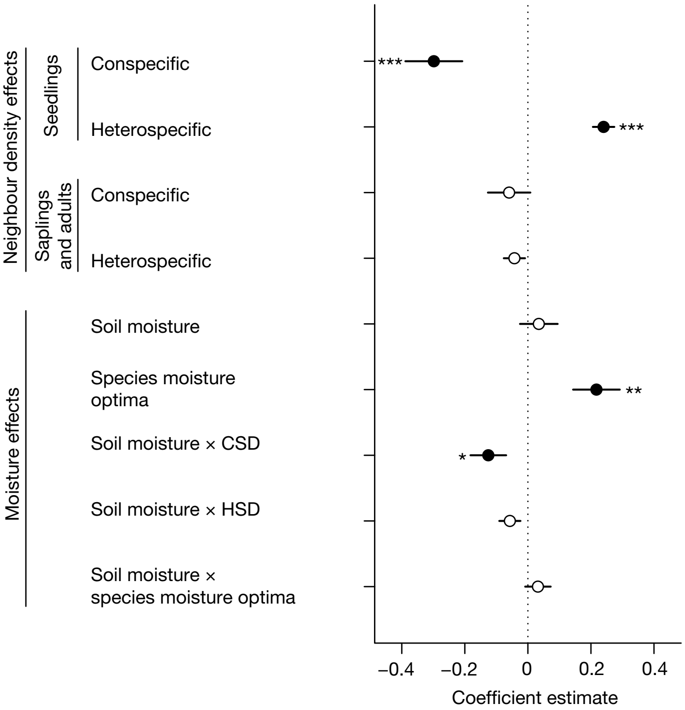


Fig. 2 | Mean effects of conspecific and heterospecific neighbours, soil moisture and SPMO on first-year seedling survival. Estimates are based on a GLMM fit to survival records of $n = 45{,}100$ seedlings recruited between 1995 and 2015 in 800 census plots, each with an area of $1\ \mathrm{m}^2$, distributed across a 50-ha forest dynamics plot (Methods). Error bars show s.e.m. Filled symbols indicate significant effects (two-tailed Wald z-tests), and asterisks indicate significance (exact P values (top to bottom): 0.0010, 1.56×10^{-12}, 0.3770, 0.2034, 0.5615, 0.0033, 0.0265, 0.0886 and 0.4310). High CSD values strongly reduce seedling survival, and this effect increases with increasing soil moisture during the wet season, as indicated by the significant negative interaction between these variables. As expected at our relatively moist site, survival is higher for species whose abundance peaks at moist sites (indicated by the SPMO). See Extended Data Fig. 3a,b for the final best-fit GLMM results and Supplementary Discussion for a discussion of HSD effects.

sensitivities determined experimentally[7]. We modelled survival over the first year of life for each seedling as a function of $\mathrm{SM_w}$, SPMO, the interaction between $\mathrm{SM_w}$ and SPMO, the density of conspecific seedling neighbours (CSD), the density of heterospecific seedling neighbours (HSD), the density of conspecific sapling and adult or large neighbours (CLD), the density of heterospecific sapling and adult or large neighbours (HLD), and the interactions between $\mathrm{SM_w}$ with HSD and CSD. We focus on the interactions between $\mathrm{SM_w}$ and seedling densities (CSD and HSD) because the effect of seedling neighbours is an order of magnitude stronger than the effects of larger neighbours in our dataset[33,34] and because the interactions between $\mathrm{SM_w}$ and larger neighbour densities did not improve our model (Methods). The interactions between $\mathrm{SM_w}$ and CSD and between $\mathrm{SM_w}$ and SPMO address the two mechanisms that are hypothesized to affect diversity. A negative interaction between $\mathrm{SM_w}$ and CSD would be consistent with the hypothesis that wetter years reduce survival when CSDs are high or strengthen CNDD. A positive interaction between $\mathrm{SM_w}$ and SPMO would be consistent with the physiological tolerance hypothesis, with wetter years enhancing survival of moisture-sensitive species. As the study site is near the wet end of the rainfall gradient used to quantify SPMO, we also expected greater survival among species with higher values of SPMO[7].

The strongest effect on first-year survival was a negative effect associated with CSD as observed previously[33,34] (Fig. 2). We refer to this effect as seedling CNDD. The interaction between soil moisture content and CSD ($\mathrm{SM_w} \times$ CSD) was also significantly negative (Fig. 2). Wetter years enhanced seedling CNDD (Fig. 3a and Extended Data Fig. 3c). A direct positive effect of soil moisture availability on survival was only evident at the lowest CSDs (Fig. 3b,c). The interaction between soil moisture and CSD reversed the expected positive relationship between survival and soil moisture at higher CSDs (Fig. 3b,d). The interaction between soil moisture and CSD advantages locally rare species during wetter years and could thereby contribute to the greater diversity of first-year survivors in wetter years (Fig. 1). In modern coexistence theory, the relative strengths of CNDD and heterospecific neighbour density dependence (HNDD) influence population stabilization and species coexistence[31,32]. We assess the relative strength of CNDD and HNDD at different soil moisture levels in the Extended Data Fig. 4 and the Supplementary Discussion.

The significant, positive effect of SPMO on first-year survival indicates greater survival among species whose abundance peaks in moist sites, as expected at our relatively moist site (Fig. 2). A significant, positive interaction between soil moisture and SPMO ($\mathrm{SM_w} \times$ SPMO) would provide evidence consistent with the physiological tolerance hypothesis. This interaction was positive as expected but not significant (Fig. 2). Thus, increased survival of moisture-sensitive species seems to be unlikely to contribute significantly to the greater diversity of first-year survivors in wetter years (Fig. 1).

We explored alternative models in which $\mathrm{SM_w}$ is replaced with mean soil moisture during the dry season ($\mathrm{SM_d}$) or across both seasons ($\mathrm{SM_b}$). The data did not support these alternative models (difference

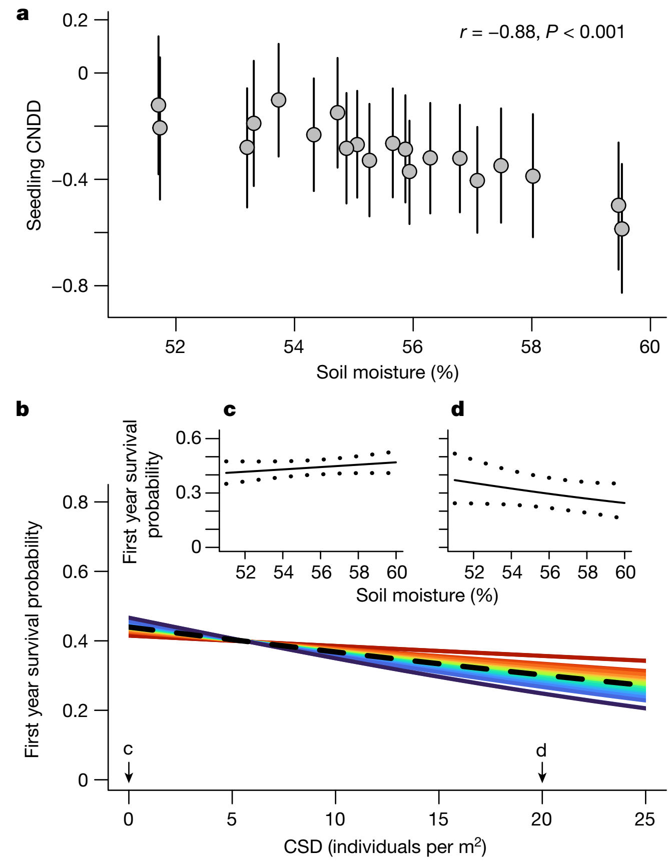


Fig. 3 | Relationships between soil moisture, conspecific seedling neighbour effects and first-year seedling survival. **a**, The estimated strength of CNDD associated with CSD (seedling CNDD) increased significantly with mean wet season soil moisture across 20 seedling cohorts (Pearson's *r*; two-sided *t*-test, $P = 4.395 \times 10^{-7}$). Mean effects are calculated from the coefficients of the GLMM fitted to first-year survival records of n = 45,100 seedlings recruited between 1995 and 2015 in 800 census plots, each with an area of 1 m^2, distributed across a 50-ha forest dynamics plot (Methods). Uncertainties in the estimated strength of seedling CNDD were obtained from 10,000 simulations of model parameters (see Methods). Data are mean ± 95% confidence interval. **b**, The fitted relationships between survival and CSD for the 20 seedling cohorts demonstrate the interaction between mean wet season soil moisture and conspecific neighbours. Soil moisture increases in the direction red (driest), orange, yellow, green, blue (wettest). The black dashed line represents survival with soil moisture and all other fixed effects set to their medians. Arrows along the horizontal axis correspond to the low and high CSDs in **c** and **d**, respectively. **c**,**d**, The fitted relationships (and 95% confidence intervals) between first-year survival probability and soil moisture at low CSD (no conspecific neighbours) (**c**) and high (85th percentile) CSD (**d**), show that increased soil moisture favours seedling survival at low CSD and decreases seedling survival at high CSD.

in Akaike information criterion of 42 and 8, respectively). Fitted model coefficients were similar for GLMMs using SM_w, SM_d and SM_b, with one exception (Extended Data Table 1). The fitted coefficient for the interaction between soil moisture and CSD was not significant for SM_d (−0.07 ± 0.05 (mean ± s.e.m.)), significant for SM_b (−0.10 ± 0.06), and notably stronger for SM_w (−0.14 ± 0.05). Wet season conditions determined the strength of the interaction between CSD and soil moisture.

We used the final best-fit model for individual-level survival to parameterize three simulations of community-level diversity of first-year survivors (see Methods). The three simulations emulated natural conditions and evaluated the relative contributions of enhanced survival of moisture-sensitive species and stronger seedling CNDD in wetter years to changes in community-level diversity of first-year survivors (Fig. 1). Simulated mean changes in diversity reproduced the observed relationship between soil moisture and percentage change in cohort diversity when all model coefficients were equal to their best-fit values (Fig. 4a,b and Extended Data Fig. 2a,b,e) and when the SM_w × SPMO coefficient was set to zero (Fig. 4a,c and Extended Data Fig. 2a,c,f). By contrast, when the SM_w × CSD coefficient was set to zero, the relationship between soil moisture and percentage change in diversity was significantly weaker (Fig.4a,d and Extended Data Fig. 2a,d,g). These simulation results are consistent with the hypothesis that the increase in seedling CNDD with soil moisture (Fig. 3a) causes the positive relationship observed between soil moisture and diversity (Fig. 1).

Seedling dynamics shape the structure of future forests[35]. To further evaluate the relevance of seedling CNDD for forest diversity, we tested whether changes in cohort diversity over the first year of seedling life endure and whether future cohort diversity is better predicted by cohort diversity at the time of recruitment or after one year. Cohort diversity after the first year was strongly correlated with future cohort diversity for at least 15 years ($r \geq 0.7$; Extended Data Fig. 5a). Compared with cohort diversity at recruitment, cohort diversity after the first year also significantly improved the prediction of future cohort diversity (Extended Data Fig. 5b). Thus, the observed changes in diversity during the first year of seedling life have long-lasting effects.

Several mechanisms might contribute to seedling CNDD[36]. We discount intraspecific competition for light, water and nutrients because the small leaves and root systems of first-year seedlings rarely overlap other seedlings, precluding competition for light and soil resources[33,37,38]. Furthermore, competition for water should be reduced, and not enhanced, in wetter soils (Fig. 3a) and should occur during the dry season, when water availability is lowest. Yet, 20 years of natural variation in dry season soil moisture (SM_d) had no significant overall effects on seedling survival (Extended Data Table 1, bottom row). By contrast, wet season soil moisture was associated with stronger seedling CNDD (Fig. 3), with long-lasting effects on seedling diversity (Fig. 4). Natural enemies disperse between seedlings and soils with higher moisture facilitate the dispersal and virulence of some enemies. Specifically, soil microorganisms—including primary pathogenic fungi and oomycetes—infect healthy seedlings, cause seedling CNDD in tropical forests[12,14–18,26], and often respond to increased moisture availability with increases in transmission and/or virulence[11,24–26]. Experiments will be necessary to evaluate the possible link between primary pathogens, soil moisture availability and the strength of seedling CNDD (Fig. 3a).

Ecologists have investigated the causes of the increase in tropical tree diversity along rainfall gradients by focusing on the relative contributions of drought stress and natural enemies. The experimental evidence for stronger enemy-mediated CNDD along rainfall gradients is limited[36,39]. The significant interaction between temporal variation in soil moisture and the strength of seedling CNDD in our study suggests the reasons for this limited evidence. Reciprocal transplant studies in which a single seedling of each species is planted in each experimental plot[40,41] capture the direct physiological effects of drought that we observed for low CSDs (Fig. 3b,c) but miss the strong indirect biotic effect of moisture availability that we observed for high CSDs (Fig. 3b,d). By contrast, reciprocal transplant studies in which seedlings are planted with conspecific neighbours showed more damage and mortality from pathogens at the wetter site for most species[42]. More generally, interactions between abiotic and biotic factors such as those observed here between soil moisture and CNDD can explain why climate variables are often weak predictors of tree mortality patterns[43].

The effects of soil moisture on CNDD and diversity may extend to anthropogenic drivers that affect soil moisture, including forest fragmentation, forest degradation and climate change. Simplified forest structure and edge effects significantly reduce soil moisture[44,45] and

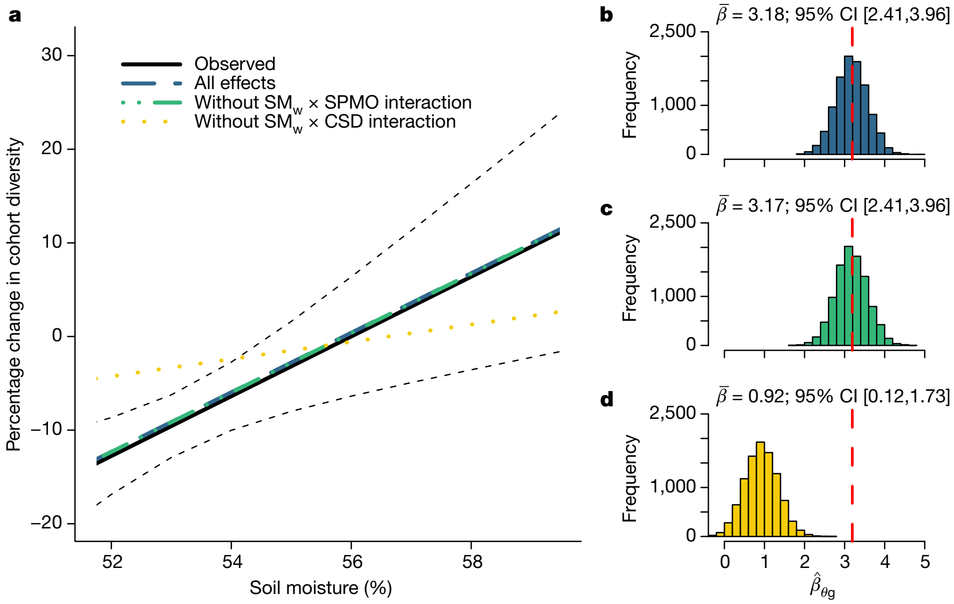


Fig. 4 | Observed and simulated relationships between soil moisture and changes in cohort diversity. a, The relationship for changes observed over the first year of seedling life (from Fig. 1) is indistinguishable from relationships simulated using all fitted coefficients from the individual-level survival model or simulated using all fitted coefficients except the interaction between soil moisture and SPMO ($\mathrm{SM_w}$ × SPMO). The relationship for changes simulated using all fitted coefficients except the interaction between soil moisture and CSD ($\mathrm{SM_w}$ × CSD) is significantly weaker. See Methods for details on modelling communities and fitting the relationship. **b**–**d**, The observed slope of the relationship (vertical red dashed line), the distribution of simulated slopes and means ($\bar{\beta}$) and 95% confidence interval (CI) for simulated slopes including all coefficients from the individual-level survival model (**b**) and all coefficients except the $\mathrm{SM_w}$ × SPMO interaction (**c**) or the $\mathrm{SM_w}$ × CSD interaction (**d**). Changes in diversity are expressed as the percentage change in the effective number of species (${}^2D$). The pattern is qualitatively similar for ${}^1D$ (Extended Data Fig. 2a–d).

could cause declines in diversity by reducing the strength of CNDD as demonstrated in this study. Experiments on the importance of CNDD in forest fragments anticipate this by showing that fungi- and insect-mediated CNDD promote diversity in the forest interior but not on its drier edges[46]. Forest fragmentation and degradation are likely to reduce plant diversity through effects on soil moisture that weaken CNDD.

Climate change is altering moisture availability across the tropics, increasing the urgency to understand its effects on tropical forest diversity[27,47]. Our long-term records of temporal variation in moisture, seedling survival and diversity show that weaker CNDD tends to preserve local dominance and low seedling diversity in drier years, whereas stronger CNDD tends to reduce local dominance and increase seedling diversity in wetter years (Figs. 1 and 3a). We have shown that the temporal variation in CNDD is associated with moisture availability[48,49] and is a community-wide phenomenon with persistent impacts on diversity (Extended Data Fig. 5), as first hypothesized 50 years ago for variation in conspecific density-dependent interactions and diversity along spatial moisture gradients[3,4]. Most tropical tree species regenerate from a persistent, shade-tolerant seedling bank. Conspecific density-dependent effects are strongest at this life stage, and a depauperate seedling bank is unlikely to sustain a diverse community[35,50]. The relationships between temporal variation in moisture availability, the strength of CNDD and diversity documented here suggest that tree species diversity will be affected as climate change and anthropogenic disturbance alter moisture availability in tropical forests.

Online content

Any methods, additional references, Nature Portfolio reporting summaries, source data, extended data, supplementary information, acknowledgements, peer review information; details of author contributions and competing interests; and statements of data and code availability are available at https://doi.org/10.1038/s41586-023-05717-1.

1. Gentry, A. H. Changes in plant community diversity and floristic composition on environmental and geographical gradients. *Ann. Missouri Bot. Gard.* **75**, 1–34 (1988).
2. Givnish, T. J. On the causes of gradients in tropical tree diversity. *J. Ecol.* **87**, 193–210 (1999).
3. Janzen, D. H. Herbivores and the number of tree species in tropical forests. *Am. Nat.* **104**, 501–528 (1970).
4. Connell, J. H. in *Dynamics of Populations* (eds Den Boer, P. J. & Gradwell, G. R.) 298–312 (PUDOC, 1971).
5. Esquivel-Muelbert, A. et al. Seasonal drought limits tree species across the Neotropics. *Ecography* **40**, 618–629 (2017).
6. Gillett, J. B. Pest pressure, an underestimated factor in evolution. *Syst. Assoc. Publ.* **4**, 37–46 (1962).
7. Engelbrecht, B. M. J. et al. Drought sensitivity shapes species distribution patterns in tropical forests. *Nature* **447**, 80–82 (2007).
8. Condit, R., Engelbrecht, B. M. J., Pino, D., Pérez, R. & Turner, B. L. Species distributions in response to individual soil nutrients and seasonal drought across a community of tropical trees. *Proc. Natl Acad. Sci. USA* **110**, 5064–5068 (2013).
9. Allen, C. D. et al. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *For. Ecol. Manage.* **259**, 660–684 (2010).
10. Harrison, S., Spasojevic, M. J. & Li, D. Climate and plant community diversity in space and time. *Proc. Natl Acad. Sci. USA* **117**, 4464–4470 (2020).
11. Milici, V. R., Dalui, D., Mickley, J. G. & Bagchi, R. Responses of plant–pathogen interactions to precipitation: Implications for tropical tree richness in a changing world. *J. Ecol.* **108**, 1800–1809 (2020).
12. Mangan, S. A. et al. Negative plant-soil feedback predicts tree-species relative abundance in a tropical forest. *Nature* **466**, 752–755 (2010).
13. Gripenberg, S. et al. Testing for enemy-mediated density-dependence in the mortality of seedlings: field experiments with five Neotropical tree species. *Oikos* **123**, 185–193 (2014).
14. Bagchi, R. et al. Pathogens and insect herbivores drive rainforest plant diversity and composition. *Nature* **506**, 85–88 (2014).
15. Fricke, E. C., Tewksbury, J. J. & Rogers, H. S. Multiple natural enemies cause distance-dependent mortality at the seed-to-seedling transition. *Ecol. Lett.* **17**, 593–598 (2014).
16. Augspurger, C. K. & Kelly, C. K. Pathogen mortality of tropical tree seedlings: experimental studies of the effects of dispersal distance, seedling density, and light conditions. *Oecologia* **61**, 211–217 (1984).
17. Chen, L. et al. Differential soil fungus accumulation and density dependence of trees in a subtropical forest. *Science* **366**, 124–128 (2019).
18. Eck, J. L., Stump, S. M., Delavaux, C. S., Mangan, S. A. & Comita, L. S. Evidence of within-species specialization by soil microbes and the implications for plant community diversity. *Proc. Natl Acad. Sci. USA* **116**, 7371–7376 (2019).
19. Kishimoto-Yamada, K. & Itioka, T. How much have we learned about seasonality in tropical insect abundance since Wolda (1988)? *Entomol. Sci.* **18**, 407–419 (2015).
20. Huberty, A. F. & Denno, R. F. Plant water stress and its consequences for herbivorous insects: a new synthesis. *Ecology* **85**, 1383–1398 (2004).

21. Janzen, D. H. & Hallwachs, W. To us insectometers, it is clear that insect decline in our Costa Rican tropics is real, so let's be kind to the survivors. *Proc. Natl Acad. Sci. USA* **118**, e2002546117 (2021).
22. Rodríguez-Castañeda, G. The world and its shades of green: a meta-analysis on trophic cascades across temperature and precipitation gradients. *Glob. Ecol. Biogeogr.* **22**, 118–130 (2013).
23. Janzen, D. H. & Schoener, T. W. Differences in insect abundance and diversity between wetter and drier sites during a tropical dry season. *Ecology* **49**, 96–110 (1968).
24. Sturrock, R. N. et al. Climate change and forest diseases. *Plant Pathol* **60**, 133–149 (2011).
25. Desprez-Loustau, M.-L., Marçais, B., Nageleisen, L.-M., Piou, D. & Vannini, A. Interactive effects of drought and pathogens in forest trees. *Ann. For. Sci.* **63**, 597–612 (2006).
26. Swinfield, T., Lewis, O. T., Bagchi, R. & Freckleton, R. P. Consequences of changing rainfall for fungal pathogen-induced mortality in tropical tree seedlings. *Ecol. Evol.* **2**, 1408–1413 (2012).
27. Jactel, H. et al. Drought effects on damage by forest insects and pathogens: a meta-analysis. *Glob. Chang. Biol.* **18**, 267–276 (2012).
28. Maharjan, S. K. et al. Plant functional traits and the distribution of West African rain forest trees along the rainfall gradient. *Biotropica* **43**, 552–561 (2011).
29. Klironomos, J. N. Feedback with soil biota contributes to plant rarity and invasiveness in communities. *Nature* **417**, 67–70 (2002).
30. Petermann, J. S., Fergus, A. J. F., Turnbull, L. A. & Schmid, B. Janzen–Connell effects are widespread and strong enough to maintain diversity in grasslands. *Ecology* **89**, 2399–2406 (2008).
31. Chesson, P. Updates on mechanisms of maintenance of species diversity. *J. Ecol.* **106**, 1773–1794 (2018).
32. Barabás, G., Michalska-Smith, M. J. & Allesina, S. The effect of intra- and interspecific competition on coexistence in multispecies communities. *Am. Nat.* **188**, E1–E12 (2016).
33. Lebrija-Trejos, E., Wright, S. J., Hernández, A. & Reich, P. B. Does relatedness matter? Phylogenetic density-dependent survival of seedlings in a tropical forest. *Ecology* **95**, 940–951 (2014).
34. Lebrija-Trejos, E., Reich, P. B., Hernández, A. & Wright, S. J. Species with greater seed mass are more tolerant of conspecific neighbours: a key driver of early survival and future abundances in a tropical forest. *Ecol. Lett.* **19**, 1071–1080 (2016).
35. Green, P. T., Harms, K. E. & Connell, J. H. Nonrandom, diversifying processes are disproportionately strong in the smallest size classes of a tropical forest. *Proc. Natl Acad. Sci. USA* **111**, 18649–18654 (2014).
36. Comita, L. S. et al. Testing predictions of the Janzen–Connell hypothesis: a meta-analysis of experimental evidence for distance- and density-dependent seed and seedling survival. *J. Ecol.* **102**, 845–856 (2014).
37. Moles, A. T. & Westoby, M. What do seedlings die from and what are the implications for evolution of seed size? *Oikos* **106**, 193–199 (2004).
38. Paine, C. E. T., Harms, K. E., Schnitzer, S. A. & Carson, W. P. Weak competition among tropical tree seedlings: implications for species coexistence. *Biotropica* **40**, 432–440 (2008).
39. Weissflog, A., Markesteijn, L., Lewis, O. T., Comita, L. S. & Engelbrecht, B. M. J. Contrasting patterns of insect herbivory and predation pressure across a tropical rainfall gradient. *Biotropica* **50**, 302–311 (2018).
40. Brenes-Arguedas, T., Coley, P. D. & Kursar, T. A. Pests vs. drought as determinants of plant distribution along a tropical rainfall gradient. *Ecology* **90**, 1751–1761 (2009).
41. Gaviria, J. & Engelbrecht, B. M. J. Effects of drought, pest pressure and light availability on seedling establishment and growth: their role for distribution of tree species across a tropical rainfall gradient. *PLoS ONE* **10**, e0143955 (2015).
42. Spear, E. R., Coley, P. D. & Kursar, T. A. Do pathogens limit the distributions of tropical trees across a rainfall gradient? *J. Ecol.* **103**, 165–174 (2015).
43. Clark, J. S. et al. The impacts of increasing drought on forest dynamics, structure, and biodiversity in the United States. *Glob. Chang. Biol.* **22**, 2329–2352 (2016).
44. Riutta, T. et al. Experimental evidence for the interacting effects of forest edge, moisture and soil macrofauna on leaf litter decomposition. *Soil Biol. Biochem.* **49**, 124–131 (2012).
45. Lebrija-Trejos, E., Pérez-García, E. A., Meave, J. A., Poorter, L. & Bongers, F. Environmental changes during secondary succession in a tropical dry forest in Mexico. *J. Trop. Ecol.* **27**, 477–489 (2011).
46. Krishnadas, M. & Comita, L. S. Edge effects on seedling diversity are mediated by impacts of fungi and insects on seedling recruitment but not survival. *Front. Glob. Chang.* **2**, 76 (2019).
47. Garcia, R. A., Cabeza, M., Rahbek, C. & Araujo, M. B. Multiple dimensions of climate change and their implications for biodiversity. *Science* **344**, 1247579 (2014).
48. Uriarte, M., Muscarella, R. & Zimmerman, J. K. Environmental heterogeneity and biotic interactions mediate climate impacts on tropical forest regeneration. *Glob. Chang. Biol.* **24**, e692–e704 (2018).
49. Bachelot, B., Kobe, R. K. & Vriesendorp, C. Negative density-dependent mortality varies over time in a wet tropical forest, advantaging rare species, common species, or no species. *Oecologia* **179**, 853–861 (2015).
50. Zhu, Y. et al. Density-dependent survival varies with species life-history strategy in a tropical forest. *Ecol. Lett.* **21**, 506–515 (2018).

Methods

Study site and data collection

The study was conducted in the lowland tropical moist forest of Barro Colorado Island (BCI; 9.15° N, 79.85° W) in central Panama. Annual rainfall averages 2,600 mm, with just 10% falling during a 4-month dry season (January to April). Temperature averages 26 °C for 11 months and 27 °C in April. All seedlings of woody plants (no lower size limit imposed) were censused annually during the dry season from 1994 through 2019 for 800 1-m^2 plots located around 250 seed-trap stations in a 50-ha, old-growth forest dynamics plot (FDP)[51]. All free-standing, woody plants ≥1 cm diameter at breast height (DBH) in the FDP have been identified to species, mapped to the nearest 0.5 m, and measured for DBH every 5 years since 1985, except during 2020[52]. We used FDP census data to calculate densities of large (≥1 cm DBH) CLDs and HLDs for each realized combination of seedling species, census year, and 1-m^2 plot. For years between the 5-year FDP censuses, we linearly interpolated densities of larger plants. Thus, t ($0 \le t \le 4$) years after the FDP census in year y, the density (D) of species j was estimated as $D_{j(y+t)} = D_{jy} + 0.2 \times t \times (D_{j(y+5)} - D_{jy})$, where $D_{j(y+5)}$ refers to the density of species j in the next FDP census. The focal seedling dataset includes 45,100 fully identified recruits of 215 species with known year of recruitment between 1995 and 2015 and SPMO. The study ends in 2015 with the most recent census of the 50-ha FDP used to calculate 2 independent variables for the seedling survival analyses.

SPMO values were determined from models of occurrence probability fitted to the distributions of 550 tree species at 72 sites across a strong rainfall gradient extending from the dry Pacific to wet Caribbean coasts of central Panama[8]. Condit et al.[8] used standardized ($N(0, 1)$) cumulative dry season water deficits as a measure of dry season intensity to represent the rainfall gradient. Thus, SPMO has mean 0 and s.d. 1 and represents the water deficit at which a species attains peak probability of occurrence, with negative and positive values for species associated with drier and wetter sites, respectively. The 215 species included in our analyses encompass the entire range of SPMO values in Condit et al.[8].

We use soil moisture in our analyses because soil moisture is a direct and immediate measure of water availability to plants and soil biota. Results of alternative analyses using rainfall, a widely available climatic variable, are presented in the Supplementary Discussion.

Gravimetric soil water content (θ_g) was determined for 30–40 cm depth every two weeks between June and November and every week between December and May since 1971 for 10 locations distributed within the 9.73-ha Lutz watershed, located 1.25 km from the FDP. Kupers et al.[53] determined soil water potential (SWP) repeatedly during the dry season in 2015 and 2016 at 240 locations distributed across the 50-ha FDP. SWP is the most direct measure of water availability for plants and microorganisms. We evaluated the relationship between θ_g in the continuously monitored Lutz watershed and SWP in the 50-ha plot. We calculated mean and s.e.m. values for both sites for soil moisture measurements taken up to 4 days apart from February to April 2015 and in March 2016. Lutz θ_g and SWP in the 50-ha FDP are strongly correlated ($r = 0.80$; two-tailed t-test, $P = 0.02$; Extended Data Fig. 6). This indicates that Lutz θ_g measurements are a good predictor of moisture availability at the 50-ha FDP.

We calculated mean θ_g for each month starting with our first seedling census in 1994. Seedlings emerge between May and September on BCI[54], and we record recruitment between January and March and first-year survival between January and March one year later. We calculated mean wet season (May to December) soil moisture over two wet seasons for each seedling, including the wet season the seedling emerged and the wet season between its recruitment and first-year censuses. This is appropriate because moisture availability might affect transmission and virulence of natural enemies throughout this period. We calculated mean dry season (January to April) soil moisture for the dry season of the recruitment census. This is appropriate because rainfall during April determines the length and severity of the dry season and seedlings only experienced one April before their first-year census.

Soil moisture and species diversity

To assess effects of soil moisture on diversity, we evaluated the relationship between soil moisture and the observed change in first-year cohort diversity (Fig. 1, Extended Data Fig. 2a). A preliminary analysis using correlations and multiple regression showed that changes in diversity were most strongly related to mean soil moisture over wet season months and were not significantly related to mean soil moisture over dry season months (Extended Data Table 2). These results concur with a preliminary analysis (described below) showing greater support for a seedling survival GLMM including mean wet season soil moisture. Wet season soil moisture is used in subsequent analyses for these reasons.

We calculated relative changes in total diversity—that is, in diversity across all seedling plots combined—because our soil moisture data are from outside the census plots and are an indicator of soil moisture status for the whole area and because diversity sampling bias is likely severe at the 1-m^2 plot scale. To quantify diversity, we used Hill numbers (^qD), which indicate the number of equally common species required to give a particular value of a diversity index or true diversity[55]. The superscript q—the 'order' of the diversity—indicates the sensitivity of the Hill number to species relative frequencies. We calculated the relative change in diversity as $\Delta^qD_{t_0,t_1} = 100 \times (^qD_{t_1} - {}^qD_{t_0})/{}^qD_{t_0}$, where $^qD_{t_0}$ and $^qD_{t_1}$ represent cohort diversity at the recruitment and first-year censuses, respectively. We present changes in diversity for $q = 2$ in the main text. ^2D equals the inverse Simpson dominance index and places more weight on abundant than rare species[55]. This order of D matches our GLMM modelling approach where random effects for groups with few data (such as rare species) are influenced by the overall effect size and groups with ample data (such as abundant species). We also present changes in diversity for ^1D in Extended Data Fig. 2a–d. ^1D equals the exponential Shannon entropy index and weights species by their abundance without favouring either common or rare species.

We used generalized least squares (GLS) to evaluate the relationship between observed mean wet season soil moisture content and observed changes in diversity ($\Delta^qD_{t_0,t_1}$). GLS allows variance in the dependent variable ($\Delta^qD_{t_0,t_1}$) to increase with the independent variable (soil moisture) (that is, heteroscedastic errors; Fig.1). Models were fitted using variance structures that were either constant (homoscedastic errors) or a proportional, power or exponential function of soil moisture. Models with heteroscedastic variance structures were selected when their Akaike information criterion (AIC), was at least two units lower than the AIC of the model with homoscedastic errors[56]. Models with a heteroscedastic variance structure, a power function of soil moisture, were selected for both $\Delta^2D_{t_0,t_1}$ and $\Delta^1D_{t_0,t_1}$.

Seedling survival analysis

We used a GLMM with a binomial error distribution (logit link function) to analyse first-year survival of seedling recruits as a function of CSD and HSD, the CLD and HLD, mean soil moisture (SM) over dry, wet or both seasons combined (alternative model fits are described below), SPMO and the SM × HSD, SM × CSD and SM × SPMO interactions. We analysed subsets of our data to demonstrate that results are robust with respect to species' abundances (see Supplementary Discussion). The SM × SPMO interaction addresses the physiological tolerance hypothesis that temporal variation in soil moisture has differential effects on the survival of species with different soil moisture affinities. A positive SM × SPMO interaction would indicate that wetter years disproportionately enhanced survival of moisture-sensitive species associated with wetter forests. The SM × CSD interaction addresses the hypothesis that temporal variation in soil moisture alters seedling CNDD. A negative SM × CSD interaction indicates that wetter years strengthen seedling CNDD. We focused on the interactions between seedling neighbours and soil moisture because previous analyses indicated that seedling neighbours have an order of magnitude greater impact on survival than do larger neighbours[33,34] and because models including the SM × CLD and SM × HLD interactions performed worse than models excluding them (ΔAIC = 1.6 and 2.0, respectively, for models including SM_w), consistent with non-significant effect estimates (0.015 ± 0.061, $P = 0.81$ and -0.024 ± 0.034, $P = 0.48$; significance based on two-tailed Wald *z*-tests).

Conspecific and heterospecific neighbour densities equalled the number of woody plants <1 cm DBH in each 1-m^2 plot for seedlings and the number of free-standing, woody plants ≥1 cm DBH within 1.15 crown radii of each 1-m^2 plot for larger neighbours. Following Lebrija-Trejos et al.[33,34], we selected 1.15 crown radii for larger neighbours by using the likelihood ratio test to evaluate improvements in the likelihood of 11 models for crown radii of 1.00, 1.05, 1.10, ... 2.0. Individual crown radii were estimated from DBH and allometric relationships between DBH and crown diameter of BCI trees[57]. Lebrija-Trejos et al.[33] evaluated the performance of the variable-radius approach used in this study and concluded that models using the variable-radius approach had much greater support than models using a fixed radius to estimate neighbour densities whether with neighbours weighted equally, by basal area or by basal area divided by distance.

GLMM estimates of density-dependent effects can be biased by saturating functional responses to the density of individuals[58]. To accommodate saturating responses, we evaluated the support for models with square and fourth root transformations of CSD, HSD, CLD and HLD using the AIC (see model fitting details below). A model with the fourth root transformation of HSD was better than a model with untransformed HSD (ΔAIC = −57). Models with square or fourth root transformations of the remaining neighbour terms performed worse than models with untransformed variables (the ΔAIC between models with the best transformation for each term—$HLD^{1/2}$, $CLD^{1/2}$ and $CSD^{1/2}$—and the model with untransformed variables equalled 1, 9 and 45, respectively, for models including SM_w).

A preliminary analysis determined whether mean soil moisture during dry season months (SM_d, January to April), wet season months (SM_w, May to December) or all months combined (SM_b) should be included in the GLMM using the AIC. Fitted coefficients are qualitatively similar for all three models, and AIC was minimized using wet season soil moisture only (ΔAIC = 9 for SM_b and 43 for SM_d, Extended Data Table 1).

Model fitting details

All fitted GLMMs included random intercepts for species, year and plots (nested within seed-trap stations) to account for interspecific, interannual and spatial variation, respectively. To minimize type I error rate inflation, we followed Bolker et al.[59] and Barr et al.[60] and fitted 'maximal' GLMMs that included all possible random slopes by species and years as well as their correlations. We included random slopes for species for each fixed effect except SPMO, which is a property of species, and for year for each fixed effect except SM, which is a property of years (the best-fit maximal model is shown below). The maximal models produced a singular (boundary) fit warning, with the lme4 (v. 1.1-27.1) R package. GLMMs with complex random structures are often singular. The singular fit warning indicates that one or more of the variance-covariance Cholesky decomposition parameters (θ) are close to zero ($<10^{-4}$) or in the boundary of the allowable parameter space[61]. While singular models are statistically well defined and it is possible that the 'true' best fitting model has θ parameters that approach zero, there are concerns about the power and reliability of estimates of parameter uncertainty in such models that could compromise statistical inference[62].

Therefore, we followed the recommendations of Barr et al.[60] to simplify the random structure of the model until it converged successfully while minimizing type I statistical error. Barr et al.[60] recommend removing correlations among random terms first, removing random intercepts and slopes only if problems persist, and using a common random structure to compare models. We compared models with the following alternative fixed effects: neighbour density represented by untransformed and square and fourth root transformations of CSD, HSD, CLD and HLD; moisture availability represented by soil moisture during the wet (SM_w), dry (SM_d) and both seasons (SM_b) or by rainfall for the same seasons; and with interactions of SM_w with CLD and HLD. The maximal model that converged successfully for every alternative parameterization removed correlations among random terms by year and species and retained all random intercepts and slopes. We used this 'zero correlation' random structure and AIC to compare the relative fit of alternative models. The best-fit 'zero correlation' model with the lowest AIC included SM_w and the fourth root transformation of HSD.

To select a final 'maximal' best-fit model structure that minimizes type I error, we started with the maximal singular model including all correlations among random terms. The model equation in Wilkinson–Rogers notation[63] follows:

$$\begin{aligned}
&\text{Alive} \sim 1 + \text{CSD} + \text{HSD}^{0.25} + \text{CLD} + \text{HLD} + \text{SM}_\text{w} + \text{SPMO}\\
&+\text{SM}_\text{w} \times\ \text{CSD} + \text{SM}_\text{w} \times \text{HSD}^{0.25} + \text{SM}_\text{w} \times \text{SPMO}\\
&+(1 + \text{CSD} + \text{HSD}^{0.25} +\ \text{CLD} + \text{HLD} + \text{SM}_\text{w} + \text{SM}_\text{w} \times \text{CSD}\\
&+\text{SM}_\text{w} \times \text{HSD}^{0.25}|\text{species}) +\ (1|\text{trap/plot})\\
&+(1 + \text{CSD} + \text{HSD}^{0.25} + \text{CLD} + \text{HLD} + \text{SPMO}|\text{year}),
\end{aligned}$$

where the response variable 'Alive' indicates whether a seedling survived (Alive = 1) or died (Alive = 0) one year after recruitment; and the random grouping terms 'species', 'trap', 'plot' and 'year' are factor variables indicating the species of the focal individual, the FDP seed-trap station, the 1-m^2 seedling plot where the seedling was censused and the seedling cohort year, respectively. We removed only the terms necessary to achieve convergence without a boundary fit by removing covariances of random terms one at a time and then two at a time and three at a time until non-singular convergence was achieved. Our final best-fit GLMM excluded the correlations of HSD, SM_w × HSD and SM_w × CSD with other random terms by species and is presented in the main text as the 'final best-fit' model.

The GLMM model equation of the final model follows (the double vertical line indicates that covariances were not estimated for the random terms inside the parentheses):

$$\begin{aligned}
&\text{Alive} \sim 1 + \text{CSD} + \text{HSD}^{0.25} + \text{CLD} + \text{HLD} + \text{SM}_\text{w} + \text{SPMO}\\
&+\text{SM}_\text{w} \times \text{CSD} +\ \text{SM}_\text{w} \times \text{HSD}^{0.25} + \text{SM}_\text{w} \times \text{SPMO}\\
&+(1 + \text{CSD} + \text{CLD} + \text{HLD} + \text{SM}_\text{w}|\text{species}) +\ (0 + \text{HSD}^{0.25}\\
&+\text{SM}_\text{w} \times \text{CSD} + \text{SM}_\text{w} \times \text{HSD}^{0.25}||\text{species}) + (1|\text{trap/plot})\\
&+\ (1 + \text{CSD} + \text{HSD}^{0.25} + \text{CLD} + \text{HLD} + \text{SPMO}|\text{year}).
\end{aligned}$$

To facilitate convergence and interpretation, all independent variables were centred by subtracting their median and scaled by dividing by their interquartile range (IQR), a robust measure of variability. The IQR equals the difference between the upper and lower quartiles of the data (or between the 75th and 25th percentiles). Slopes of predictors scaled in this way can be interpreted as the change in effects from conditions with a typical 'low' (25th percentile) value to a typical 'high' (75th percentile) value of the predictor. Centring predictors further allows (conditional) main effects estimates to be equivalent among models with or without interaction terms[64]. Analyses of residuals of the final best-fit model including plots of residuals against predictors are found in Extended Data Figs. 7 and 8 and Supplementary Discussion.

Simulating effects of moisture on species diversity

We simulated expected patterns of change in first-year cohort diversity with variation in soil moisture for three scenarios. We used best-fit coefficients from our final best-fit individual-level survival model and observed values of all independent variables to calculate the survival probability of each observed seedling recruit (*P*) for each scenario. The first scenario retained all model coefficients to emulate observed conditions. The second scenario set the $SM_w \times SPMO$ coefficient to zero to evaluate the role of differential survival of moisture-sensitive species with increased moisture. The final scenario set the $SM_w \times CSD$ coefficient to zero to evaluate the role of enhanced seedling CNDD with increased moisture. We simulated a cohort of first-year survivors by comparing the survival probabilities (P) calculated for each observed recruit to random draws (r) from a uniform distribution bounded between 0 and 1. Simulated individuals survived the first year when $P \geq r$ and died otherwise. We calculated the diversity of each simulated cohort of first-year survivors (${}^qD_{t_1(\mathrm{sim})}$) and the change in diversity relative to the observed cohort of seedling recruits $\Delta^qD_{t_0,t_1(\mathrm{sim})} = 100 \times ({}^qD_{t_1(\mathrm{sim})} - {}^qD_{t_0})/{}^qD_{t_0}$. We repeated this procedure for the 20 observed cohorts of seedling recruits and calculated the linear regression slope (see next paragraph) and Spearman correlation between the 20 values of $\Delta^qD_{t_0,t_1(\mathrm{sim})}$ and observed mean soil moisture contents. Finally, we compared the observed and 10,000 simulated values for slopes (Fig. 4 and Extended Data Fig. 2b–d) and Spearman correlations (Extended Data Fig. 2e–g) for each scenario.

As with the relationship between observed soil moisture content and observed changes in diversity, we used GLS with different variance structures to fit linear regressions to the relationship between observed soil moisture content and mean simulated changes in diversity ($\Delta^qD_{t_0,t_1(\mathrm{sim})}$) for the three simulated scenarios (Fig. 4 and Extended Data Fig. 2). According to the AIC, a constant variance structure was selected for all mean simulated changes in diversity ($\Delta^qD_{t_0,t_1(\mathrm{sim})}$) except the mean simulated change in ${}^1D$ for the scenario zeroing the $SM_w \times CSD$ coefficient, where a power (of soil moisture) variance structure was selected. We also fit linear regressions between observed soil moisture content and simulated $\Delta^qD_{t_0,t_1(\mathrm{sim})}$ for each simulated set of 20 cohorts. Models for each of the simulated sets of 20 cohorts were fitted with the same variance structure selected for the models involving mean simulated changes.

Species diversity through time

We performed two tests to evaluate the lasting importance of first-year changes in diversity. First, we evaluated the persistence of first-year changes in diversity through time (Extended Data Fig. 5a). Second, we determined whether cohort diversity at the time of recruitment or after the first year was more strongly correlated with the diversity of the same cohort two through 10 years later (Extended Data Fig. 5b). Because these analyses do not require the FDP census data, we used seedling cohorts from 1995 through 2019. To test for the persistence of first-year changes in diversity through time, we evaluated the decay of Pearson correlation coefficients calculated between cohort diversity after one year and cohort diversity after 2 through 15 years. We set a maximum of 15 years to maintain a minimum of 10 first-year cohorts to calculate correlation coefficients. Ten is the minimum sample size to determine whether a correlation differs from zero with a significance level $\alpha = 0.05$, a statistical power $1 - \beta = 0.85$ and an alternative hypothesis of $r = 0.8$ (a strong correlation)[65]. For the second test, we calculated Pearson correlation coefficients between cohort diversity at recruitment or after 1 year and cohort diversity after 2 through 10 years and tested for a significant difference in correlation strength. We used a one-tailed Dunn and Clark's test, which is based on Fisher's r-to-z transform and is appropriate for comparing two dependent correlations (those obtained from the same observations and having one variable in common)[66]. We set a maximum of 10 years to maintain a minimum of 15 cohorts to test for differences in correlation strength[66]. With seedlings censused through 2019, 15 cohorts (1995 to 2009) were followed for 10 or more years.

We conducted all modelling analyses in R v. 3.6.0 (ref. [67]), using the lme4 (ref. [61]) (v.1.1-27.1) and nlme[68] (v.3.1-153) packages for GLMM and GLS models, respectively. Parameter simulations ($n = 10{,}000$) used to compute uncertainties in the estimated strength of seedling CNDD (Fig. 3a) were performed with the sims function of the arm package[69] (v.1.12-2). Analyses of residuals were performed with the arm and DHARMa[70] (v. 0.4.5) packages.

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

All datasets generated or analysed during the current study are available through Figshare repositories. The first-year seedling survival and diversity datasets, including soil water availability and rainfall[71] are available at https://figshare.com/s/a4d2dbb2a73b3eb09f9f. The FDP SWP source data[72] are available at https://doi.org/10.6084/m9.figshare.c.4372898.v1, and the Lutz Watershed soil water content[73] is available at https://doi.org/10.25573/data.10042517.v2.

Code availability

An R script demonstrating the model fitting routine and containing code to reproduce main and supplementary analyses of the study is available in the Figshare repository at https://figshare.com/s/a4d2dbb2a73b3eb09f9f[71].

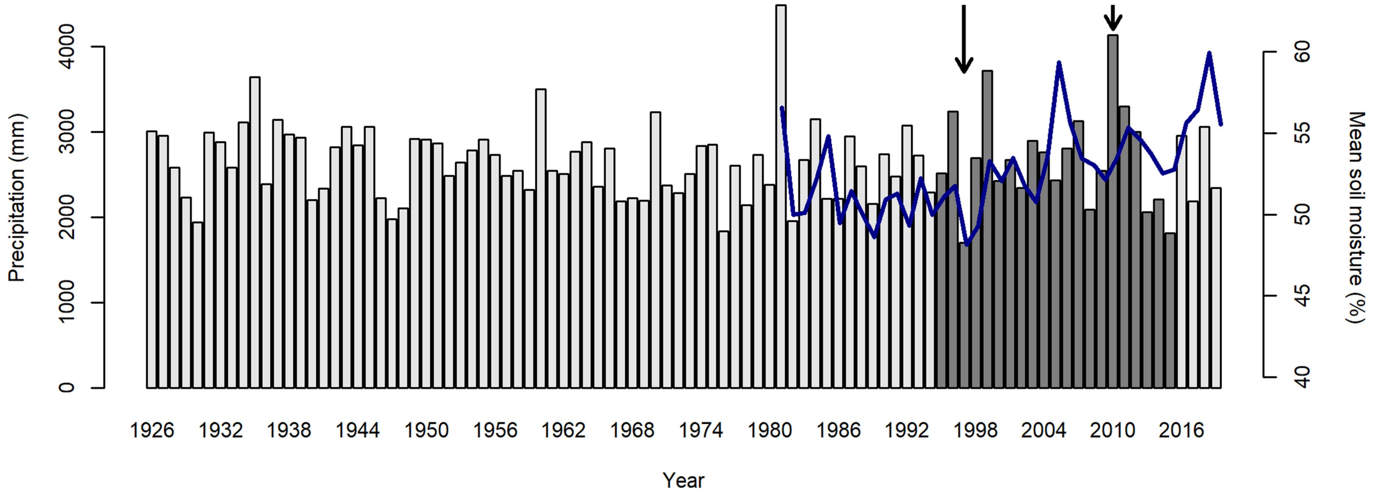
51. Wright, S. J., Calderón, O., Hernandéz, A. & Muller-Landau, H. C. Annual and spatial variation in seedfall and seedling recruitment in a neotropical forest. *Ecology* **86**, 848–860 (2005).
52. Condit, R. *Tropical Forest Census Plots* https://doi.org/10.1007/978-3-662-03664-8 (Springer, 1998).
53. Kupers, S. J., Wirth, C., Engelbrecht, B. M. J. & Rüger, N. Dry season soil water potential maps of a 50 hectare tropical forest plot on Barro Colorado Island, Panama. *Sci. Data* **6**, 63 (2019).
54. Garwood, N. C. in *The Ecology of a Tropical Forest: Seasonal Rhythms and Long-term Changes* (eds Leigh, E. G., Rand, A. S. & Windsor, D. M.) 173–185 (Smithsonian Institution Press, 1982).
55. Jost, L. Entropy and diversity. *Oikos* **113**, 363–375 (2006).
56. Burnham, K. P. & Anderson, D. R. *Model Selection and Multimodel Inference* https://doi.org/10.1007/b97636 (Springer, 2004).
57. Muller-Landau, H. C. et al. Testing metabolic ecology theory for allometric scaling of tree size, growth and mortality in tropical forests. *Ecol. Lett.* **9**, 575–588 (2006).
58. Detto, M., Visser, M. D., Wright, S. J. & Pacala, S. W. Bias in the detection of negative density dependence in plant communities. *Ecol. Lett.* **22**, 1923–1939 (2019).
59. Bolker, B. M. et al. Generalized linear mixed models: a practical guide for ecology and evolution. *Trends Ecol. Evol.* **24**, 127–135 (2009).
60. Barr, D. J., Levy, R., Scheepers, C. & Tily, H. J. Random effects structure for confirmatory hypothesis testing: keep it maximal. *J. Mem. Lang.* **68**, 255–278 (2013).
61. Bates, D., Mächler, M., Bolker, B. & Walker, S. Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* **67**, 1–48 (2015).
62. Bates, D. et al. *Package 'lme4' Reference Manual* https://cran.r-project.org/web/packages/lme4/lme4.pdf (2021).
63. Wilkinson, G. N. & Rogers, C. E. Symbolic description of factorial models for analysis of variance. *Appl. Stat.* **22**, 392 (1973).
64. Afshartous, D. & Preston, R. A. Key results of interaction models with centering. *J. Stat. Educ.* https://doi.org/10.1080/10691898.2011.11889620 (2011).
65. Cohen, J. *Statistical Power Analysis for the Behavioral Sciences* https://doi.org/10.1016/C2013-0-10517-X (Elsevier, 1977).
66. Steiger, J. H. Tests for comparing elements of a correlation matrix. *Psychol. Bull.* **87**, 245–251 (1980).
67. R Core Team. *R: A Language and Environment for Statistical Computing* https://www.R-project.org/ (2016).
68. Pinheiro, J. et al. *nlme: Linear and Nonlinear Mixed Effects Models* https://CRAN.R-project.org/package=nlme (2020).
69. Gelman, A. & Hill, J. *Data Analysis Using Regression and Multilevel/Hierarchical Models* (Cambridge Univ. Press, 2007).
70. Hartig, F. *DHARMa: Residual Diagnostics for Hierarchical (Multi-level/Mixed) Regression Models* https://CRAN.R-project.org/package=DHARMa (2021).
71. Lebrija-Trejos, E., Wright, S. J. & Hernández, A. *Moisture, Density-dependent Interactions, and Tropical Tree Diversity* https://figshare.com/s/a4d2dbb2a73b3eb09f9f (2022).
72. Kupers, S. J., Wirth, C., Engelbrecht, B. M. J. & Rüger, N. *Dry Season Soil Water Potential Maps of a 50 Hectare Tropical Forest Plot on Barro Colorado Island, Panama* https://doi.org/10.6084/m9.figshare.7611005.v1 (2019).
73. Paton, S. *Barro Colorado Island, Lutz Catchment, Soil Moisture, Manual* https://doi.org/10.25573/data.10042517.v1 (2019).

Acknowledgements The authors thank H. Muller-Landau for comments that improved the manuscript, and G. Barabás and M. M. Mayfield for their insights into species coexistence theory. The BCI forest dynamics plot was founded by S. P. Hubbell and R. B. Foster and is now managed by S. Davies, R. Condit, S. Lao and R. Perez. Numerous organizations provided funds for the FDP, principally the US National Science Foundation and the Smithsonian Institution. E.L.-T. thanks Oranim College of Education for funds to visit S.J.W. at STRI. The Environmental Sciences Program of the Smithsonian Institution funded seedling censuses from 1995 through 2008. This research was supported by grant no. 2017044 from the United States–Israel Binational Science Foundation (BSF). Computations of GLMMs were performed on the Hive computer cluster at the University of Haifa, partly funded by ISF grant 2155/15.

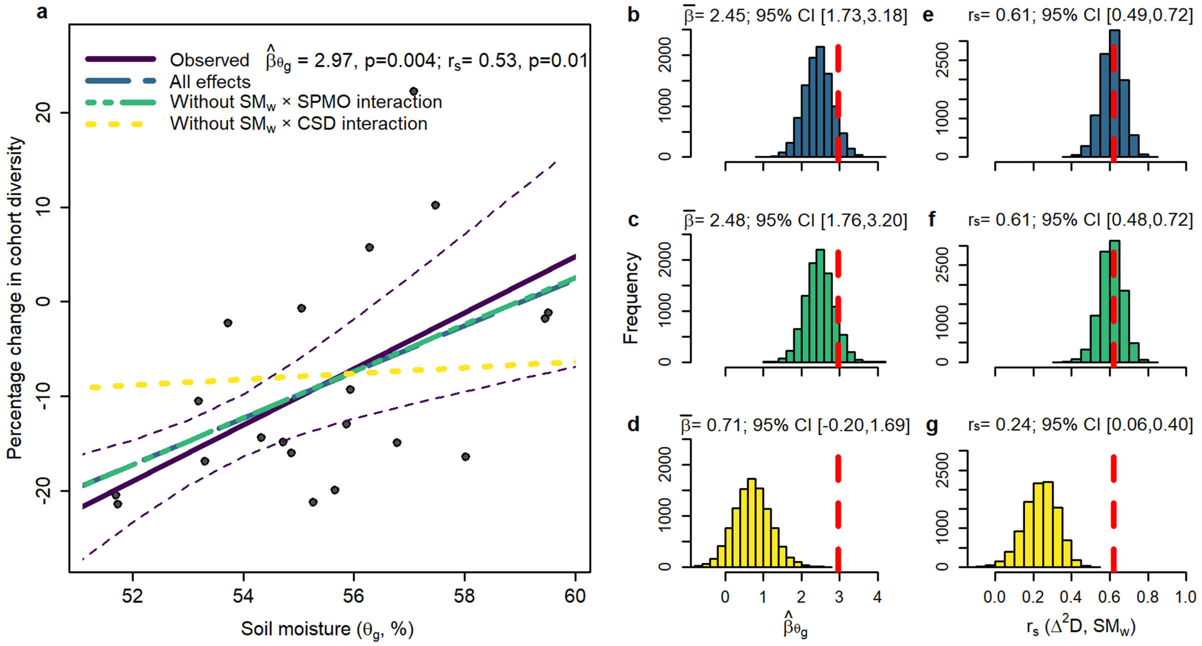
Author contributions E.L.-T. conceived and conducted the analyses in this study and led writing. S.J.W. designed and maintained censuses for 26 years and contributed to analyses and writing. A.H. supervised data collection and identified seedlings.

Competing interests The authors declare no competing interests.

Additional information
Supplementary information The online version contains supplementary material available at https://doi.org/10.1038/s41586-023-05717-1.
Correspondence and requests for materials should be addressed to Edwin Lebrija-Trejos.
Peer review information *Nature* thanks Lisa Hülsmann, Owen Lewis and the other, anonymous, reviewer(s) for their contribution to the peer review of this work. Peer reviewer reports are available.



Extended Data Fig. 1 | Annual precipitation and mean soil moisture. Precipitation records at Barro Colorado Island (BCI; 9.15°N, 79.85°W) from 1926 to 2019. Dark gray bars show precipitation during the study period (1995–2015). Black arrows mark years with the lowest (1997) and second highest (2010) precipitation since BCI rainfall records began. The continuous blue line shows annual mean soil moisture content (%) from 1981 to 2019. Monthly mean soil moisture and rainfall are significantly correlated (ties-corrected Spearman's rho = 0.63, p-value $< 2.2 \times 10^{-16}$, two-tailed asymptotic-*t* approximation test with 416-2 df). The study of first-year survival ends in 2015 with the most recent census of the 50-ha Forest Dynamics Plot used to quantify two independent variables for the survival analyses. The study of the persistence of first-year changes in diversity continues through 2019.



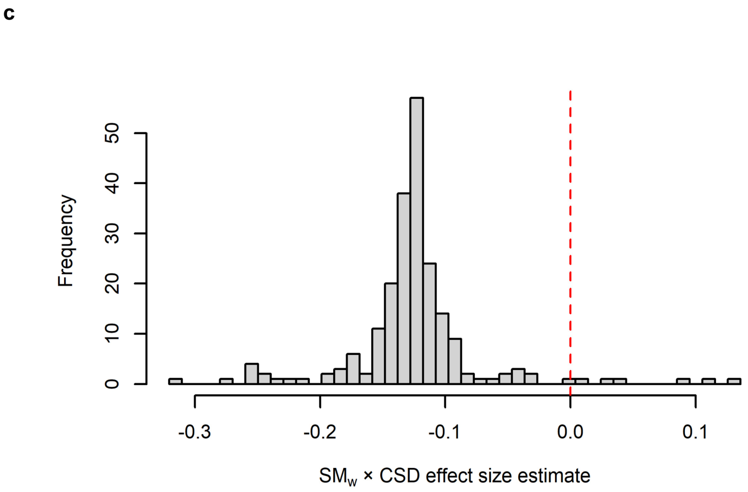
Extended Data Fig. 2 | Observed and simulated relationships between mean wet-season soil moisture (SM_w) and changes in cohort diversity over the first year of seedling life (Δ^qD) for the effective number of species or Hill numbers 1D (a–d) and ^{2}D (e–g). Panels **a–d** contain the information in main text Figs. 1 and 4 for ^{1}D. **a**. The relationship for observed changes (black dots and line with 95% confidence intervals shown as dashed black lines) is not different than that for changes simulated using all fitted coefficients from the final individual-level survival model (blue dashed line) or simulated using all fitted coefficients except the interaction between soil moisture and species-specific moisture optima (SM_w × SPMO; two dot-dash green line). The relationship for changes simulated using all fitted coefficients except the interaction between soil moisture and conspecific seedling density (SM_w × CSD; dotted yellow line) is significantly weaker. Panels, **b**,**c** and **d** show the observed slope of the relationship (vertical red dashed line), the distributions of 10,000 simulated slopes and means ($\bar{\beta}$) and 95% confidence intervals (CI) of simulated slopes including all fitted coefficients from the individual-level survival model (**b**) and all fitted coefficients except the SM_w × SPMO interaction (**c**) and the SM_w × CSD interaction (**d**). The observed slope ($\hat{\beta}_{\theta_g}$) and Spearman correlation (r_s) for the SM_w-Δ^1D relationship are in the legend of panel **a**; the two-sided p-values of a t-test, for $\hat{\beta}_{\theta_g}$, and the AS89 algorithm, for r_s, indicate both parameters differ significantly from zero. Panels **e**, **f** and **g**, show Spearman correlation coefficients (r_s) between SM_w and simulated changes in ^{2}D. The dashed red line shows the observed r_s for 20 seedling cohorts. Histograms show distributions of 10,000 simulated r_s values. The observed correlation does not differ from simulated correlations that emulated natural conditions by retaining all best-fit coefficients of our individual-level survival model (**e**) or that zeroed the interaction between wet-season soil moisture (SM_w) and species-specific moisture optima (SPMO) to evaluate the role of differential survival of moisture-sensitive species with greater soil moisture (**f**). In contrast, the observed correlation differs from simulated correlations that zeroed the interaction between SM_w and the density of conspecific seedling neighbours (CSD) to evaluate the role of enhanced conspecific seedling negative density dependence with soil moisture (**g**). See Methods for detailed descriptions of the simulations, seedling survival model, calculations of changes in diversity and fitting of linear models.

a

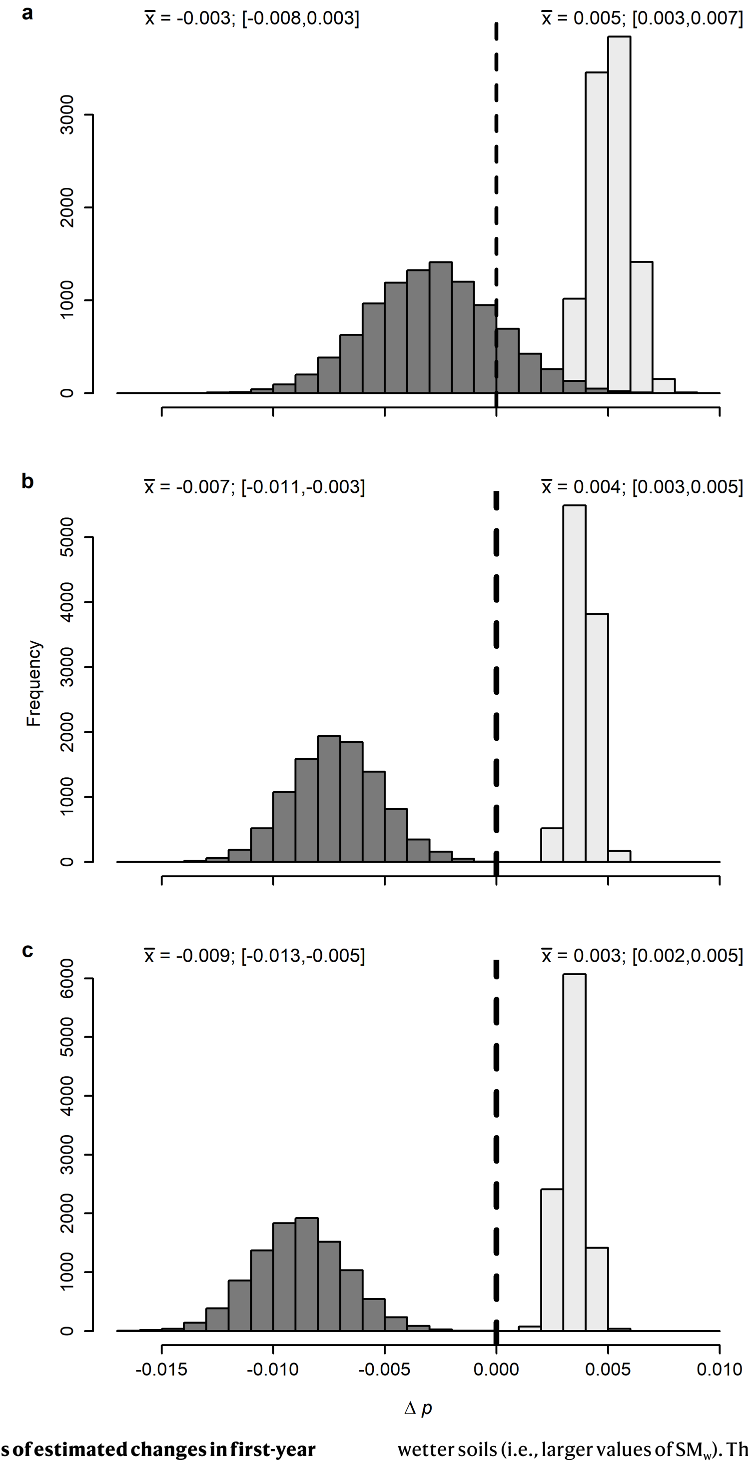
Fixed factor	Estimate	SE	z - value	*P* – value
Intercept	-0.33	0.09	-3.54	4.0e-04 ***
Conspecific seedling density (CSD)	-0.30	0.09	-3.31	0.001 ***
Heterospecific seedling density (HSD)	0.24	0.03	7.07	1.6e-12 ***
Conspecific large density (CLD)	-0.06	0.07	-0.88	0.377 ns
Heterospecific large density (HLD)	-0.04	0.03	-1.27	0.203 ns
Mean wet-season soil moisture (SM_w)	0.03	0.06	0.58	0.561 ns
Species moisture optima (SPMO)	0.22	0.07	2.94	0.003 **
Mean wet-season soil moisture × Conspecific seedling density (SM_w × CSD)	-0.13	0.06	-2.22	0.027 *
Mean wet-season soil moisture × Heterospecific seedling density (SM_w × HSD)	-0.06	0.03	-1.70	0.089 ns
Mean wet-season soil moisture × Species moisture optima (SM_w × SPMO)	0.03	0.04	0.79	0.431 ns

b

Grouping factor	Random effect	SD
Species	Intercept	0.980
	CSD	0.553
	HSD	0.131
	CLD	0.400
	HLD	0.092
	SM_w	0.243
	SM_w × CSD	0.198
	SM_w × HSD	0.058
Year	Intercept	0.180
	CSD	0.072
	HSD	0.086
	CLD	0.062
	HLD	0.089
	SPMO	0.081
Plot	Intercept	0.348
Trap	Intercept	0.154

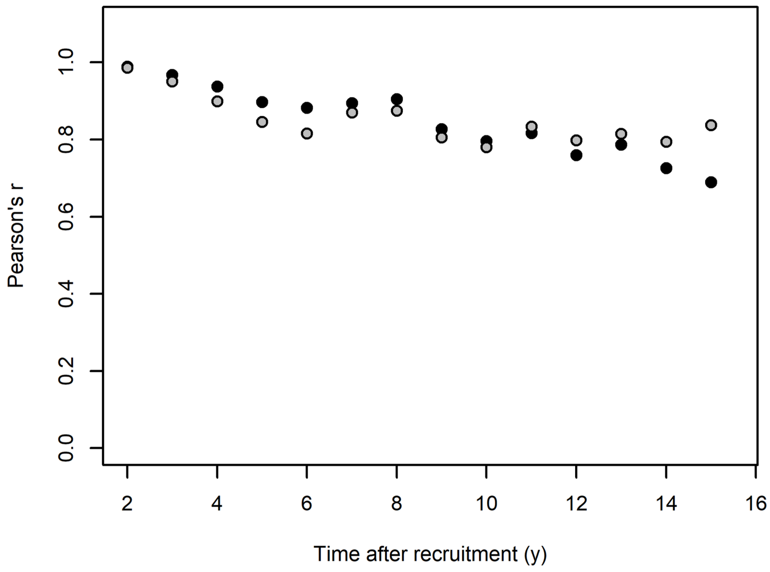


Extended Data Fig. 3 | Summary of results of the final best-fit generalized linear mixed model of first year seedling survival using wet season soil moisture. **a**. Estimate, standard error (SE) and significance of fixed effects (two-tailed Wald-Z tests). Seedling density quantifies all individuals < 1 cm DBH found in the same 1-m^2 plot with the focal seedling. Large density quantifies all individuals ≥ 1 cm DBH found within 1.15 crown radii of the seedling plot. With median centred variables, the exponential of the intercept indicates the mean first year survival odds, $y = P/(1 - P)$, where P = survival probability, when fixed effects are set to their medians. The exponential of the fixed effect coefficients indicates the proportional change in first year survival odds with one interquartile range (IQR) increase in the predictor. The slopes of the main effects of predictors involved in interactions indicate the change in the first-year survival odds with a one IQR increase in the predictor when the second predictor in the interaction is at its median value. **b**. Estimates of the standard deviation (SD) of random effects; SD values are in the same scale as the fixed effects estimates in **a** thus allowing the comparison of their magnitudes. **c**. Species-specific (random effect) estimates of the effect of the interaction between conspecific seedling density (CSD) and mean wet-season soil moisture (SM_w). Negative values indicate a strengthening of negative CSD effects with increasing SM_w. Only 7 out of 215 species are estimated to experience reduced conspecific seedling negative density dependence with increasing SM_w.



Extended Data Fig. 4 | Distributions of estimated changes in first-year survival probability (Δ *p*) with one unit increases in HSD (light bars) or CSD (dark bars) at a) low, b) median and c) high values of soil moisture (i.e., 25, 50 and 75 percentiles of SM_w). The distributions fulfil the conditions for potential species stabilization under the assumptions of Modern Coexistence Theory (i.e., CNDD > HNDD) for all values of SM_w with stronger effects for wetter soils (i.e., larger values of SM_w). The estimates of the difference in effects between CSD and HSD include the observed main effect of seedling density and its interactions with $SM_{w,}$ with other predictors set at their median values. The mean ($\bar{x}$) and 95% confidence intervals (in square brackets) of Δ *p* for each seedling density effect are shown above the corresponding distribution.

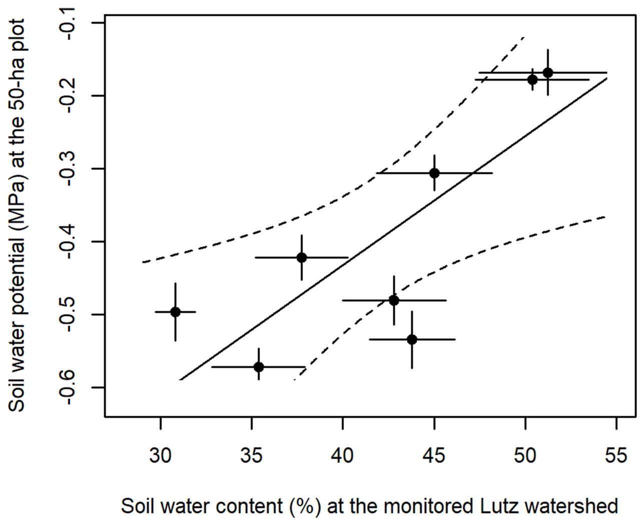
a



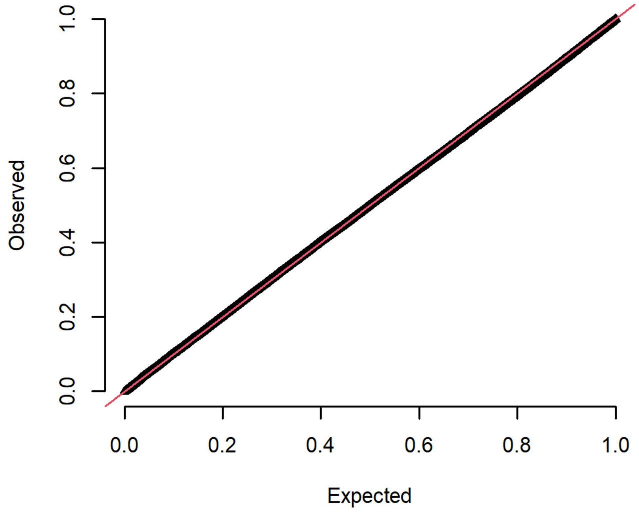
b

Cohort age (years)	Coefficient of determination (r^2)		Difference in variation explained (%)	z - value	*P* – value (one tail)	*N*
	with first year diversity	with recruit diversity				
Diversity quantified as ^{2}D						
2	0.97	0.88	9	-5.42	2.9×10^{-08}	23
3	0.90	0.79	12	-3.91	4.6×10^{-05}	22
4	0.81	0.68	13	-3.29	5.1×10^{-04}	21
5	0.72	0.58	14	-2.86	2.1×10^{-03}	20
6	0.67	0.53	13	-2.59	4.8×10^{-03}	19
7	0.76	0.71	4	-0.84	0.19998	18
8	0.77	0.74	3	-0.52	0.30321	17
9	0.65	0.64	1	-0.21	0.41706	16
10	0.61	0.59	2	-0.31	0.37776	15
Diversity quantified as ^{1}D						
2	0.98	0.83	15	-8.37	2.8×10^{-17}	23
3	0.94	0.77	17	-5.54	1.5×10^{-08}	22
4	0.88	0.69	19	-4.31	8.1×10^{-06}	21
5	0.81	0.58	22	-4.39	5.7×10^{-06}	20
6	0.78	0.55	23	-4.18	1.5×10^{-05}	19
7	0.80	0.68	12	-1.94	0.02628	18
8	0.82	0.72	10	-1.55	0.06103	17
9	0.69	0.60	8	-1.11	0.13400	16
10	0.64	0.56	8	-0.92	0.17973	15

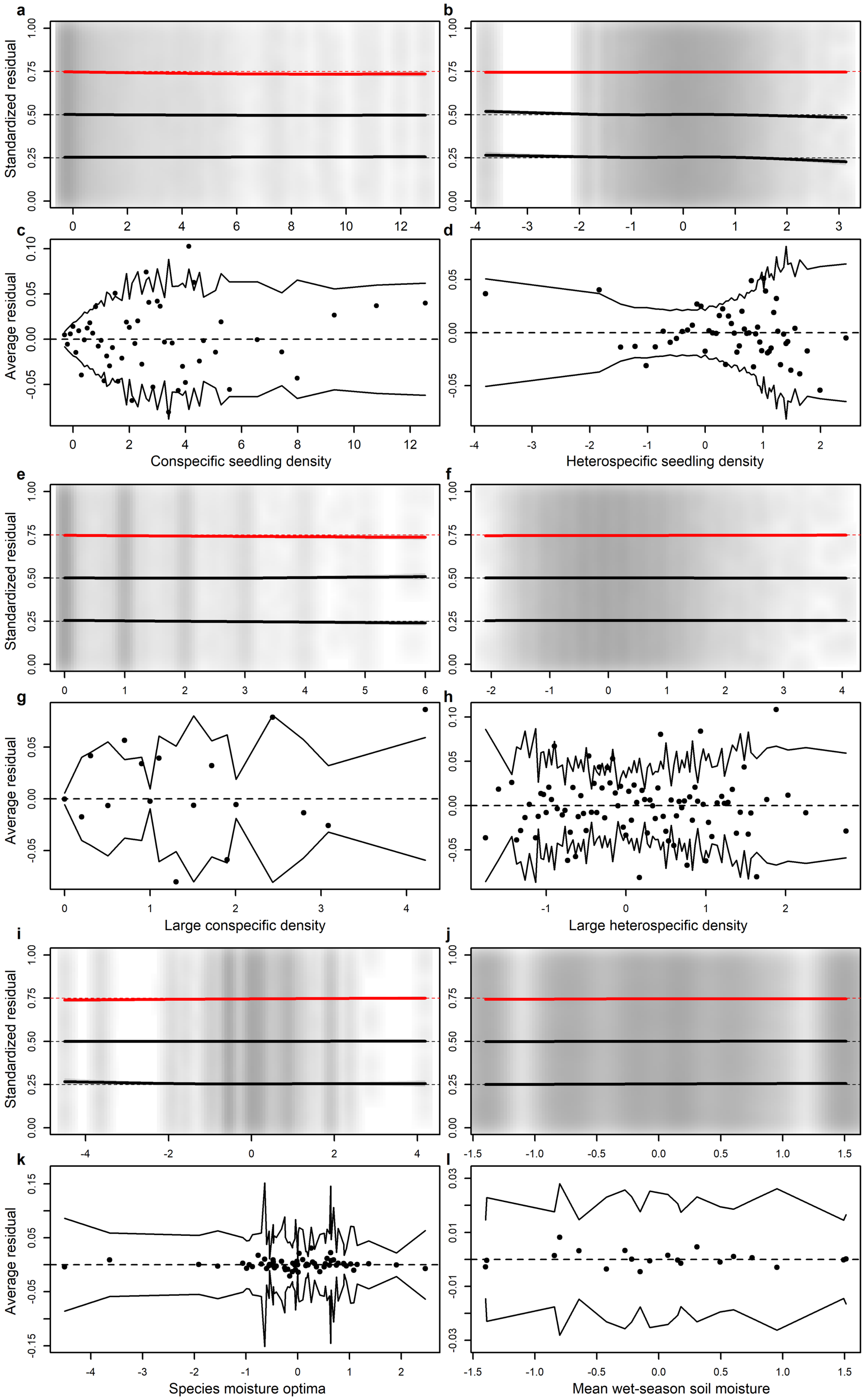
Extended Data Fig. 5 | Lasting significance of first-year changes in seedling diversity. a. Persistence of first-year changes in diversity through time. Pearson correlation coefficients (*r*) between first-year seedling cohort diversity and the diversity of the same seedling cohort two through 15 years after recruitment indicate changes in first-year cohort diversity are lasting. The number of cohorts (*N*) included in the correlation ranged from 23 to 10, respectively. Black and grey symbols represent correlations with diversity quantified by Hill numbers ^qD for q = 1 and 2, respectively. All *r* values are significant (two-sided *t* test $p < 0.028$). **b.** Results of analysis to determine whether future cohort diversity at cohort ages 2 through 10 years is better predicted by cohort diversity at the time of recruitment or one year later. Coefficients of determination (r^2) and their difference (fourth column) are presented for relationships between cohort diversity at ages 2 through 10 years and cohort diversity at the year of recruitment (third column) and after 1 year (second column). We use the Dunn and Clark z statistic to test for significant differences in the magnitude of dependent correlations (i.e., obtained from the same observations and having one variable in common, which is diversity at age *x*; See Methods) estimated for a minimum sample size (*N*) of 15 cohorts. Diversity is quantified by Hill numbers ^{2}D (upper table) and ^{1}D (lower table).



Extended Data Fig. 6 | Covariation between dry-season gravimetric soil water content in the Lutz watershed and soil water potential in the 50-ha forest dynamics plot at Barro Colorado Island. The two sites are 1.25 km apart. Pearson correlation coefficient $r = 0.80$ (two-sided t test $p = 0.018$). Kupers et al.[51]. measured soil water potential (SWP) during the dry season for samples collected across the 50-ha FDP repeatedly in 2015 and 2016. Gravimetric soil water content (θ_g) in the Lutz watershed was determined from samples taken every week between December and May across 10 sites separated by 30 to 470 m. Means (+/− s.e.m.) were calculated for measurements made less than four days apart around February 20 and 27, March 20 and 30, and April 2 and 13 in 2015 and March 11 and 16 in 2016. There were $n = 44$, 200, 119, 125, 129, 174, 112 and 217 widely scattered SWP determinations from the 50-ha FDP per measurement period, respectively, and $n = 10$ θ_g determinations from the Lutz watershed for each measurement period excepting 20 March 2015 and 16 March 2016 when $n = 9$.



Extended Data Fig. 7 | Quantile-quantile plot of scaled conditional residuals for the final best-fit first-year seedling survival model produced with the 'DHARMa' package. Kolmogorov-Smirnov test for deviations of scaled residuals from the expected uniform (flat) distribution, D45100= 0.006, two-tailed p = 0.111.



Extended Data Fig. 8 | See next page for caption.

Extended Data Fig. 8 | Conditional residuals against predictors. a,**b**,**e**,**f**,**i**,**j**, Smoothed scatterplots of zero-to-one standardized residuals produced with the 'DHARMa' package show estimated quantile regressions on the empirical 0.25, 0.5 and 0.75 distribution quantiles (continuous lines) to assist with inspection of deviations from the theoretical quantile expectations (dashed straight lines). Standard error bounds for the predicted quantile regression are too narrow to be seen. Plot shading reflects the density of data points, which are omitted for clarity. Red lines indicate significant deviations from the theoretical expectations for a uniform distribution of residuals. **c**,**d**,**g**,**h**,**k**,**l**, Binned plots of averaged residuals against predictors produced with the 'arm' package. The solid lines show plus and minus two standard errors and are expected to contain ~95% of the binned residuals. The predictor variables are scaled and transformed as used in model fitting. The number of bins was set to default values corresponding to the minimum of the square root of the sample size (i.e., 45,100 seedling recruits) or the number of unique values of the predictor (e.g., 20 unique values of mean wet-season soil moisture yields 20 bins in panel **l**).

Extended Data Table 1 | Fixed effect estimates and information criteria metrics for seedling survival GLMMs fitted with alternative soil moisture variables

SM metric included in model	Fixed effect estimate																		
	Int	Neighbour effects				Moisture effects													ΔAIC
		CSD	HSD	CLD	HLD	SM_w	SM_b	SM_d	Sp Mo	SM_w: CSD	SM_b: CSD	SM_d: CSD	SM_w: HSD	SM_b: HSD	SM_d: HSD	SM_w: SpMo	SM_b: SpMo	SM_d: SpMo	
Wet season only (SM_w)	**-0.33** ***	**-0.29** **	**0.24** ***	-0.13 *	-0.04 ns	0.05 ns	—	—	**0.21** **	**-0.14** *	—	—	-0.05 ns	—	—	0.04 ns	—	—	0
Both wet and dry seasons (SM_b)	**-0.32** ***	**-0.29** **	**0.24** ***	-0.13 *	-0.04 ns	—	0.05 ns	—	**0.21** **	—	**-0.10** *	—	—	-0.03 ns	—	—	0.04 ns	—	9
Dry season only (SM_d)	**-0.32** ***	**-0.30** **	**0.24** ***	-0.14 *	-0.04 ns	—	—	0.06 ns	**0.20** **	—	—	-0.06 ns	—	—	-0.01 ns	—	—	0.04 ns	43

Fitted GLMMs excluded correlations among random terms by species and year (see Supplementary Methods). Significant effects (two-tailed Wald-Z tests) are marked in bold. Asterisks indicate significance levels (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$). Ns = not significant. Int = model intercept; CSD = conspecific seedling density; HSD = heterospecific seedling density; CLD = conspecific large neighbour density; HLD heterospecific large neighbour density; SM_w, SM_d and SM_b = soil moisture for wet, dry and both seasons combined, respectively; SpMo = species specific moisture optima. The colon symbol denotes interactions between terms. ΔAIC= difference in Akaike Information Criteria. Exact p values of model coefficients follow. For the wet season only model, Int = 0.0001, CSD = 0.0032, HSD = 4.91×10^{-13}, CLD = 0.0169, HLD = 0.2531, SM_w = 0.4463, SpMo = 0.0081, SM_w:CSD = 0.0110, SM_w:HSD: 0.1457 and SM_w:SpMo = 0.4093. For the both seasons model, Int = 0.0002, CSD = 0.0030, HSD = 1.52×10^{-12}, CLD = 0.0167, HLD = 0.2476, SM_b = 0.2966, SpMo = 0.0083, SM_b:CSD = 0.0289, SM_b:HSD = 0.2854 and SM_b:SpMo = 0.2513. For the dry season only model, Int = 0.0003, CSD = 0.0031, HSD = 6×10^{-12}, CLD = 0.0164, HLD = 0.2374, SM_d = 0.1194, SpMo = 0.0100, SM_d:CSD = 0.2066, SM_d:HSD = 0.7768 and SM_d:SpMo = 0.1441.

Extended Data Table 2 | Relationships between changes in cohort diversity over the first year of life and seasonal mean soil moisture

a. Spearman correlation coefficients	Change in diversity ^{1}D	^{2}D
Wet season only	**0.53 (0.018)**	**0.62 (0.004)**
Dry season only	0.40 (0.085)	0.45 (0.051)
Wet and dry seasons combined	**0.51 (0.024)**	**0.57 (0.010)**

b. Multiple regression models	Effect estimate	Std. Error	t-value	p-value
^{1}D				
(Intercept)	-178.12	39.96	-4.46	0.000
Mean wet-season soil moisture	**2.55**	**1.20**	**2.13**	**0.048**
Mean dry-season soil moisture	0.57	0.91	0.63	0.539
^{2}D				
(Intercept)	-186.77	50.20	-3.72	0.017
Mean wet-season soil moisture	**3.78**	**1.50**	**2.52**	**0.022**
Mean dry-season soil moisture	-0.51	1.52	-0.44	0.664

Changes in cohort diversity are quantified by Hill numbers (^{q}D) for q=1 (^{1}D) and 2 (^{2}D). **a**. Spearman correlation coefficients, r_s, for the relationship between changes in cohort diversity over the first year of life and seasonal mean soil moisture. Correlations with soil moisture are estimated for mean soil moisture over wet and dry seasons combined and over the wet and dry seasons alone (n=20 cohorts). *P* values (two-sided t tests) for the null hypothesis that the true r_s equals zero are reported in parentheses. Significant correlations are marked in bold. **b**. Parameter estimates of generalized least squares (GLS) multiple regression models of relative changes in cohort diversity over the first year of life as a function of soil moisture averaged over wet and dry seasons separately.

nature portfolio

Corresponding author(s): Edwin Lebrija Trejos

Last updated by author(s): Nov 3, 2022

Reporting Summary

Nature Portfolio wishes to improve the reproducibility of the work that we publish. This form provides structure for consistency and transparency in reporting. For further information on Nature Portfolio policies, see our Editorial Policies and the Editorial Policy Checklist.

Statistics

For all statistical analyses, confirm that the following items are present in the figure legend, table legend, main text, or Methods section.

n/a	Confirmed	
☐	☒	The exact sample size (n) for each experimental group/condition, given as a discrete number and unit of measurement
☐	☒	A statement on whether measurements were taken from distinct samples or whether the same sample was measured repeatedly
☐	☒	The statistical test(s) used AND whether they are one- or two-sided *Only common tests should be described solely by name; describe more complex techniques in the Methods section.*
☐	☒	A description of all covariates tested
☐	☒	A description of any assumptions or corrections, such as tests of normality and adjustment for multiple comparisons
☐	☒	A full description of the statistical parameters including central tendency (e.g. means) or other basic estimates (e.g. regression coefficient) AND variation (e.g. standard deviation) or associated estimates of uncertainty (e.g. confidence intervals)
☐	☒	For null hypothesis testing, the test statistic (e.g. F, t, r) with confidence intervals, effect sizes, degrees of freedom and P value noted *Give P values as exact values whenever suitable.*
☒	☐	For Bayesian analysis, information on the choice of priors and Markov chain Monte Carlo settings
☐	☒	For hierarchical and complex designs, identification of the appropriate level for tests and full reporting of outcomes
☒	☐	Estimates of effect sizes (e.g. Cohen's d, Pearson's r), indicating how they were calculated

Our web collection on statistics for biologists contains articles on many of the points above.

Software and code

Policy information about availability of computer code

Data collection	No software was used for data collection
Data analysis	All analyses were conducted in the R software environment for statistical computing and graphics version (v.) 4.0.2, using the 'lme4' (v. 1.1-27.1) and 'nlme' (v. 3.1-153) packages for GLMM and GLS models, respectively and the 'DHARMA' (v. 0.4.5) and 'arm' (v. 1.12-2) packages from parameter simulations and residual analyses.

For manuscripts utilizing custom algorithms or software that are central to the research but not yet described in published literature, software must be made available to editors and reviewers. We strongly encourage code deposition in a community repository (e.g. GitHub). See the Nature Portfolio guidelines for submitting code & software for further information.

Data

Policy information about availability of data

All manuscripts must include a data availability statement. This statement should provide the following information, where applicable:

- Accession codes, unique identifiers, or web links for publicly available datasets
- A description of any restrictions on data availability
- For clinical datasets or third party data, please ensure that the statement adheres to our policy

All datasets generated or analysed during the current study are available in Figshare. The first-year seedling survival and diversity datasets, including summaries of soil water availability and rainfall are available with the identifier [DOI...]. The FDP soil water potential and the Lutz Watershed soil water content are available with the identifiers [DOI...] and [DOI...].

Field-specific reporting

Please select the one below that is the best fit for your research. If you are not sure, read the appropriate sections before making your selection.

☐ Life sciences ☐ Behavioural & social sciences ☒ Ecological, evolutionary & environmental sciences

For a reference copy of the document with all sections, see nature.com/documents/nr-reporting-summary-flat.pdf

Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description	We use long-term annual survival records of 45,100 fully identified seedlings of 215 tree species, censuses of their woody plant neighbors and local measurements of soil moisture to explore relationships between seedling mortality, moisture availability and conspecific neighbor density focusing on their consequences for diversity in a tropical moist forest.
Research sample	Tropical tree seedlings censused in 800 permanent 1m sq. plots located around 250 seed-trap stations in a 50-ha, old-growth Forest Dynamics Plot (FDP) in the lowland tropical moist forest of Barro Colorado Island in central Panama. Over 420,000 free-standing, woody plants ≥1 cm diameter at breast height (DBH) censused within the 50-ha FDP (used to calculate densities of conspecific and heterospecific saplings and adults for each realized combination of 1m sq. plot and seedling species). For a detail description of the FDP site and data, see https://forestgeo.si.edu/sites/neotropics/barro-colorado-island and web links therein. Approximately 7,000 soil samples taken from 10 locations within the Lutz creek Watershed, a 9.73-ha watershed located 1.25 km from the FDP (used to estimate soil moisture). All these samples constitute one of the most spatially and temporally extensive plant dynamics and soil moisture data sets available for tropical forests worldwide.
Sampling strategy	For seedlings: all woody seedling recruits (i.e., there is no lower seedling size threshold) were censused annually during the dry season from 1994 through 2019. For sapling and adult neighbors in the 50-ha, old-growth FDP: all free-standing woody plants ≥1 cm diameter at breast height DBH were identified to species, mapped to the nearest 0.5 m, and measured for DBH in 1982, 1985, and each five years thereafter, except 2020. For soil moisture: gravimetric soil water content was determined for 30-40 cm depth from soil samples taken weekly or biweekly at ten sample locations distributed across the Lutz catchment area.
Data collection	Seedling data: all measured seedlings are tagged, identified to species and measured for height and leaf number every year between January and March by a field crew led on site by Andres Hernandez, a permanent STRI technician. FDP censuses, taking hundreds of person-days, last about a year and have been directed and supervised by STRI technicians Rolando Pérez and Salomón Aguilar. Trees with DBH <60 mm are measured with calipers. Larger stems are measured with diameter tape. See Condit 1998 for full sampling details: https://doi.org/10.1007/978-3-662-03664-8. Soil moisture data collection is currently supervised by Steven Paton from STRI's Physical Monitoring Program. Soil cores are taken at 30-40 cm depth with an 'Oakfield punch' and immediately transferred to pre-weighed metal sampling containers for subsequent processing using standard methods for gravimetric determinations of soil moisture.
Timing and spatial scale	Seedlings are censused in 800 permanent 1m sq. plots within the 50-ha FDP. Germination is concentrated in the first months of the wet season and falls to zero throughout the dry season on BCI. The dry-season census from January to March thus avoids germination during the census period and excludes ephemeral germinants that fail to establish during their first wet season. The study period starts in 1995, with the first cohort of seedlings with known establishment dates, and ends in 2015, with the most recent census of the 50-ha FDP (no census was performed in 2020). We use data from five FDP censuses (1995-2015). For years between the five-year FDP censuses, we linearly interpolated densities of larger plants so that species are assumed to die or recruit gradually through the period. Soil samples for the estimation of soil moisture are collected every two weeks between June and November and every week between December and May since 1971. The specific sampling locations are areas of approximately 1m sq. that are moved every 4-5 years (usually in January) within a larger area of approximately 5 x 5 m to reduce the effects caused by soil perturbation due to technician activity. When sample locations are moved, parallel sets of samples are taken from both old and new locations for approximately 3 months in order to assure comparability. New sites that are found to differ significantly from old sites are abandoned and a new site is chosen.
Data exclusions	Since the FDP excludes lianas and small shrubs, individuals from these growth forms have been excluded as focal seedlings but they were included along with all focal recruits in calculations of seedling neighbor densities. We have also excluded 14 free standing woody species with 696 individuals in total for which no estimate of moisture optima is available.
Reproducibility	No experiments have been conducted for this study.
Randomization	Understory seed-trap stations were located along 2.7 km of trails within the 50-ha plot at 13.5-m intervals on alternating sides of the trail and randomly between 4 and 10 m from the trail. Soil samples for moisture determination are taken randomly within the 1m sq. sampling locations yet avoiding spots that have been previously sampled.
Blinding	Blinding is not relevant for the study design.

Did the study involve field work? ☒ Yes ☐ No

Field work, collection and transport

Field conditions	Annual rainfall in Barro Colorado Island averages 2600 mm. Temperature averages 26°C for 11 months and 27°C in April. Seedling censuses take place during the dry season receiving in average just 10 % of the mean annual precipitation. FDP censuses take about a full year.
Location	Latitude: 9.15°N. Longitude: 79.85°W. Plot dimensions: 1000 x 500 m. The FDP has an elevation of 120 m in average.
Access & import/export	The Barro Colorado Island FDP is located in the Barro Colorado Nature Monument, a nature reserve under the administration of the Smithsonian Tropical Research Institute. All research activities are conducted under strict regulations seeking to minimize disturbance and in accordance with Panamanian and US government laws.
Disturbance	Trampling represents the major disturbance caused by the study. The FDP has a system of well defined trails to minimize its impact.

Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

Materials & experimental systems

n/a	Involved in the study
☒	☐ Antibodies
☒	☐ Eukaryotic cell lines
☒	☐ Palaeontology and archaeology
☒	☐ Animals and other organisms
☒	☐ Human research participants
☒	☐ Clinical data
☒	☐ Dual use research of concern

Methods

n/a	Involved in the study
☒	☐ ChIP-seq
☒	☐ Flow cytometry
☒	☐ MRI-based neuroimaging