International Journal of
Plant Biology

Brief Report

Low Mortality Rates Among Tropical Ferns

Laura Salazar [1,*], Jürgen Kluge [2], Jürgen Homeier [3] and Michael Kessler [4]

1 Biogeography and Space Ecology Research Group, Life Sciences Faculty, Universidad Regional Amazónica Ikiam, Tena 150101, Ecuador
2 Faculty of Geography, Philipps University of Marburg, 35032 Marburg, Germany; klugejuergen@gmx.de
3 Faculty of Resource Management, HAWK University of Applied Sciences and Arts, 37075 Göttingen, Germany; juergen.homeier@hawk.de
4 Department of Systematic and Evolutionary Botany, University of Zurich, 8008 Zurich, Switzerland; michael.kessler@systbot.uzh.ch
* Correspondence: inecotu@gmail.com

Abstract: Tropical ferns are underrepresented in demographic studies, despite their ecological importance in forest ecosystems. This study investigates the mortality rates of terrestrial ferns along an elevational gradient (500–4000 m a.s.l.) in Ecuador, focusing on relationships with environmental variables, community characteristics, and plant size. Over two years (2009–2011), 3213 individuals representing 88 species were monitored in 22 permanent plots across eight elevations. Mortality rates, calculated as the percentage of individuals lost annually, averaged 0.87%, with a hump-shaped trend along the gradient and a significant negative relationship with temperature. Mortality rates were positively correlated with species richness and fern density, suggesting competition may influence community structure. Larger individuals exhibited higher mortality rates, likely due to greater resource demands and exposure to environmental stressors. These findings emphasize the interplay of abiotic factors, such as elevation and temperature, and biotic interactions, including competition and herbivory, in shaping fern population dynamics. The low mortality rates observed reflect population stability, potentially linked to unique life history traits, such as extended generation times. This study provides critical insights into the demographic strategies of tropical ferns and underscores the need for long-term research to better understand their responses to environmental and biotic pressures.

Keywords: terrestrial ferns; elevational gradients; size-dependent mortality

check for updates

Citation: Salazar, L.; Kluge, J.; Homeier, J.; Kessler, M. Low Mortality Rates Among Tropical Ferns. *Int. J. Plant Biol.* **2024**, *15*, 1360–1368. https://doi.org/10.3390/ijpb15040094

Academic Editor: Adriano Sofo

Received: 13 November 2024
Revised: 12 December 2024
Accepted: 16 December 2024
Published: 18 December 2024

1. Introduction

Understanding plant population dynamics is fundamental to evolutionary and ecological botany, as well as conservation biology. Recruitment, mortality, and the resulting turnover rates and generation times are influenced by various factors, including molecular evolution, species diversification, habitat disturbance, and adaptability to environmental change [1–4]. Among these, plant mortality provides critical insights into the processes shaping community structure and ecosystem functioning.

While plant population dynamics have been extensively studied in temperate ecosystems, particularly for threatened species, and in tropical systems for trees and lianas [5,6], research on tropical herbs, especially ferns, remains limited. Mortality rates for tropical trees typically range from 1 to 3% annually [7], consistent with their long life spans and large sizes. Globally, a meta-analysis [8] shows that trees exhibit an average mortality rate of 2.9×10^{-4} d^{-1} (~1 in 3500 individuals per day) and life spans approaching ~300 years. In contrast, herbaceous plants experience much higher mortality rates, averaging 5.8×10^{-3} d^{-1} (~1 in 170 per day), corresponding to their shorter life cycles of approximately 4 years. Ferns, with a mortality rate of 3.4×10^{-3} d^{-1} (~1 in 300 per day), occupy an intermediate position, with an average life span of ~55 years [8]. These differences highlight the influence of plant size and life history traits on mortality patterns.

Intrinsic factors, such as age-related senescence [9], and extrinsic factors, including habitat disturbances, pathogen outbreaks, and climatic extremes like droughts or frost [10,11], further shape plant mortality patterns. Comprehensive studies addressing these factors in tropical herbs remain scarce, limiting our understanding of their population dynamics.

Ferns are important components of forest ecosystems, particularly in tropical and subtropical regions, contributing 6–25% of local species richness and playing significant roles in processes such as nutrient cycling and tree regeneration [12,13]. Despite their ecological importance, demographic studies of ferns are rare and predominantly focus on tree ferns or a few temperate species [14,15]. The underrepresentation of herbaceous ferns in demographic studies is partly due to methodological challenges, such as difficulties in estimating the age of non-woody plants, which lack long-lasting structures like tree rings. Additionally, rhizome decay and apical meristem renewal complicate accurate assessments of longevity and mortality rates [16]. This methodological gap has hindered the generalization of fern population dynamics across species and regions.

Studies examining fern mortality have highlighted substantial variability driven by species biology and environmental factors. For example, in New Zealand, mortality rates of five *Cyathea* species ranged from 0.7% to 3.7%, with faster-growing species exhibiting higher mortality rates [17]. Conversely, smaller herbaceous ferns, such as saxicolous species of *Asplenium*, showed much lower mortality rates, often below 1%, even in disturbed habitats [15]. These findings suggest that growth strategies and ecological conditions shape mortality patterns.

To address the critical gaps in understanding fern population dynamics, this study investigates the mortality rates of terrestrial ferns along an elevational gradient (500–4000 m a.s.l.) in Ecuador. Specifically, we aim to determine whether mortality rates exhibit a distinct elevational trend and their potential relationship with temperature, how mortality rates vary with species richness and individual density within habitats, and whether mortality rates differ across species size. By focusing on these aspects, our goal is to enhance our understanding of the demographic strategies of tropical ferns and their responses to environmental gradients. While this work does not directly address the ecological roles of ferns in shaping forest ecosystems, it provides a foundation for future studies exploring the interplay between fern population dynamics and broader ecosystem processes.

2. Materials and Methods

This study is based on data collected between 2009 and 2011 as part of a broader investigation of the relationship between fern diversity and community productivity [18]. During this period, 22 permanent plots, each measuring 20 × 20 m, were established along an elevational gradient on the eastern slope of the Andes in Napo Province, Ecuador. The gradient spanned from 500 to 4000 m a.s.l., encompassing eight elevational steps. At each elevation, three plots were established, except at 3000 m a.s.l., where only one plot was included due to the limited availability of suitable forest. The sites included lowland forests near the Napo River, montane cloud forests, and páramo vegetation interspersed with patches of *Polylepis* forest at the highest elevations. Plots within the same elevation were separated by at least 100 m to minimize spatial autocorrelation, following ecological recommendations for reducing sampling bias [19].

The selection of sites was based on the presence of well-preserved habitats along the gradient, ensuring minimal anthropogenic disturbance. As elevation and temperature (closely related) were the primary variables used for site selection, other environmental factors such as slope orientation, soil type, and microclimatic conditions were not explicitly analyzed in this study. However, these factors could be discussed in subsequent studies.

Within each plot, all terrestrial fern individuals were permanently marked using plastic tags and non-corrosive wire. Resurveys were conducted during April–July of 2010 and 2011 to track individual survival. In addition, temperature data were recorded using HOBO data loggers placed in the plots at each elevational step [20]. The mean annual temperature for each elevation was calculated based on these records and used as a predictor variable in later analyses.

Mortality was defined as the condition in which a previously marked individual was either not relocated or was found without living leaves during subsequent surveys. Mortality rates were calculated separately for each period (2009–2010 and 2010–2011) as the percentage of dead individuals relative to the total population size in each plot. Specifically, the mortality rate was calculated as the number of individuals classified as dead during the period divided by the total number of individuals recorded at the beginning of that period, multiplied by 100. Recruitment was not included in this study due to the absence of a standardized lower-size threshold for individuals. This limitation was primarily driven by the challenge of reliably identifying juvenile plants to the species level in the field.

To determine whether mortality rates exhibited a distinct elevational trend, polynomial regression analyses were performed between mortality rates and elevation. Similarly, polynomial regression was applied to assess the relationship between mortality rates and mean annual temperature.

The relationship between mortality rates and fern community characteristics was examined using simple linear regressions. Species richness was defined as the total number of terrestrial fern species recorded per plot, while density was calculated as the total number of terrestrial fern individuals per plot. Additionally, a linear regression was performed to assess the relationship between species richness and abundance.

To assess differences in mortality rates across size classes, fern individuals were first grouped into five categories based on maximum frond length: <30 cm, 30–50 cm, 50–70 cm, 70–100 cm, and >100 cm. Mortality rates were then calculated separately for each size class and study period. Finally, bar plots were created to provide side-by-side comparisons of mortality rates between the 2009–2010 and 2010–2011 periods.

Differences in mortality rates between the two study periods (2009–2010 and 2010–2011) were tested using a Chi-square test. All statistical analyses and visualizations were performed using R 4.2.2 [21]. Regression models were implemented using the stats package, and visualizations were created with the ggplot2 3.5.1 package [22]. A significance threshold of $p < 0.05$ was applied to all statistical tests.

3. Results

In total, we marked and monitored 3213 fern individuals belonging to 88 species. Of these, only 43 individuals were considered to have died within the two-year study period. During the first period (2009–2010), a total of 2392 individuals were recorded, with 26 individuals classified as deceased, resulting in a mortality rate of 1.087%. In the second period (2010–2011), 2600 individuals were observed, with 17 deaths documented, leading to a mortality rate of 0.654%. The mean annual mortality rate, calculated as the average of the mortality rates from the two periods, was 0.87%. Mortality rates in consecutive years did not differ significantly (Chi-squared = 2.21, $p = 0.137$), and given the low absolute number of deaths, the mortality data for the two years were analyzed as a whole.

Along the elevational gradient, mortality rates exhibited a hump-shaped pattern, with the highest values recorded at intermediate elevations (2500 m) and zero mortality observed at 3500 m (Figure 1a). Mortality rates also showed a significant relationship with temperature ($R^2 = 0.79$, $p = 0.018$), reflecting the variation along the gradient, and there was zero mortality at 5.5 °C (Figure 1b).

In addition, mortality rates were significantly positively correlated to both number of individuals ($R^2 = 0.70$, $p = 0.000$, Figure 2a) and fern species richness ($R^2 = 0.63$, $p = 0.017$ Figure 2b), with these two factors being highly correlated among themselves ($R^2 = 0.79$, $p = 0.003$, Figure 2c).

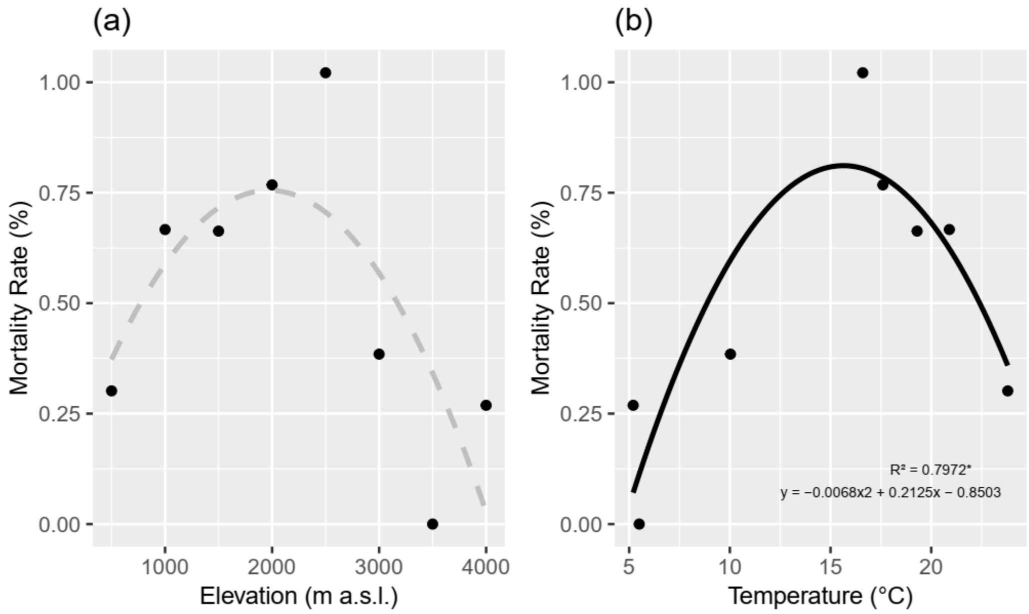

Figure 1. Relationship between mortality rate (%) of ferns and (**a**) elevation (m a.s.l.) and (**b**) temperature (°C), both modeled using second-degree polynomial regression. In both panels, the dots represent the percentage of mortality observed at different elevations. The dashed line in panel (**a**) indicates a non-significant trend, while the black line in panel (**b**) shows a significant relationship, with the equation and R^2 value displayed. The asterisks next to the R^2 value denote the level of statistical significance: * moderately significant ($p \leq 0.05$).

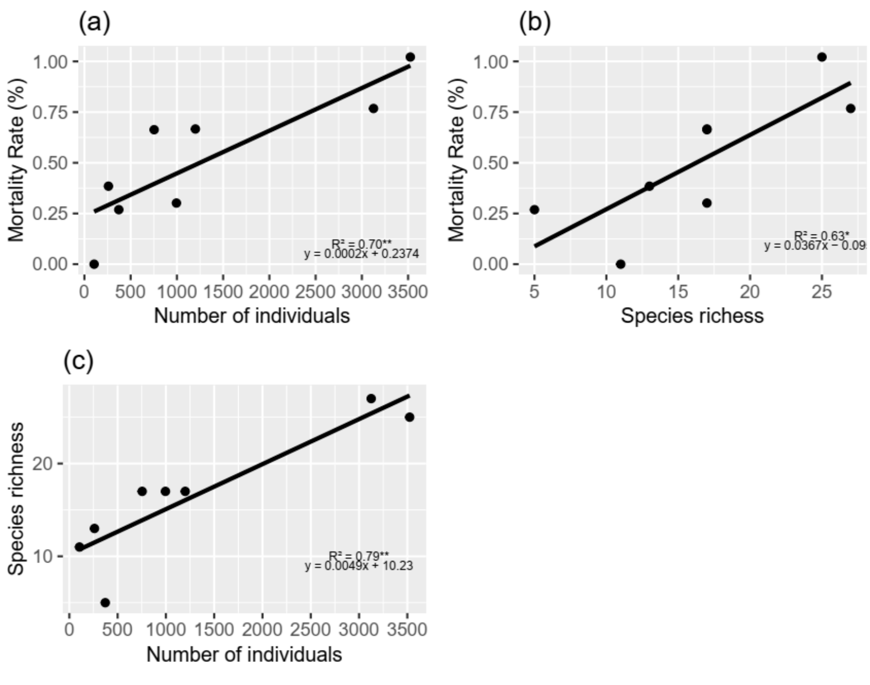

Figure 2. Relationships between (**a**) mortality rate (%) and species richness of ferns, (**b**) mortality rate (%) and number of individuals of ferns, and (**c**) species richness and number of individuals of ferns. The respective equations and R^2 values are displayed within each panel. In panels (**a**,**b**), the dots represent the percentage of mortality at specific numbers of species (**a**) or individuals (**b**). In panel (**c**), the dots represent the mean species richness and number of individuals per elevation. Only seven data points are visible in panel (**b**) due to overlapping values at different elevations. The asterisks next to the R^2 value denote the level of statistical significance: ** significant ($p \leq 0.01$), * moderately significant ($p \leq 0.05$).

Another finding of this study is that mortality rates varied significantly across size classes, with larger plants having relatively higher mortality rates and smaller plants having comparatively lower mortality rates (Figure 3). This trend was consistent over both study periods (2009–2010 and 2010–2011). The largest size class (>100 cm) had the highest mortality rates, while the smallest size class (<30 cm) consistently had the lowest mortality rates.

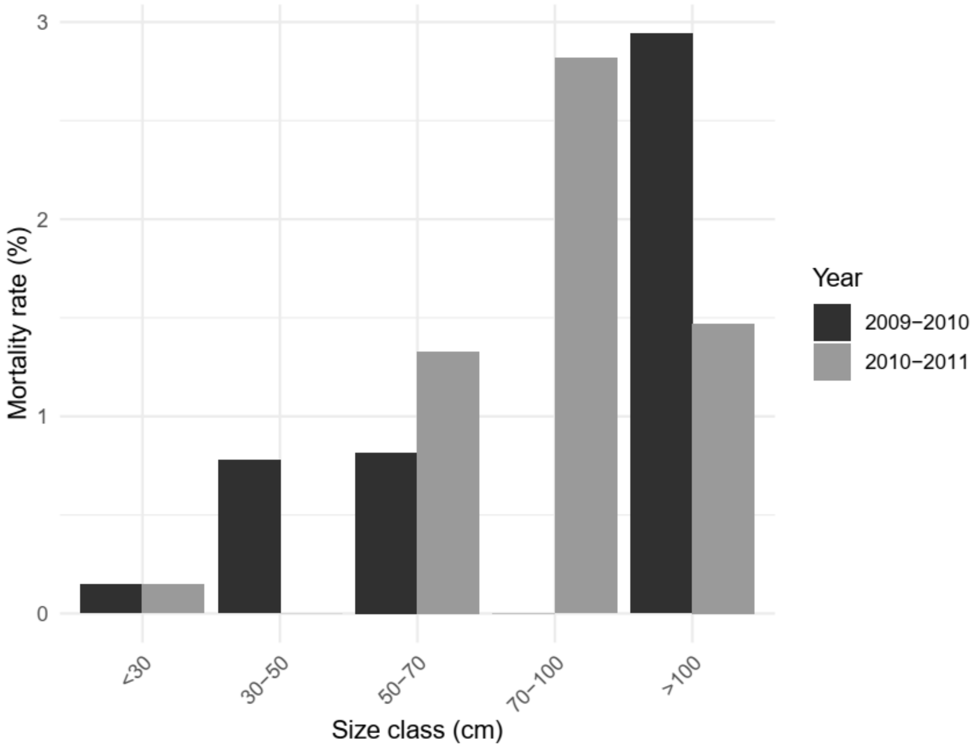

Figure 3. Mortality rate (%) of ferns by size class (cm) for 2009–2010 (darker bars) and 2010–2011 (lighter bars), categorized by leaf length: 10–30 cm, 30–50 cm, 50–70 cm, 70–100 cm, and >100 cm.

4. Discussion

To our knowledge, this is the first study to estimate the mortality rates of tropical ferns at the community level, filling a significant gap in our understanding of their population dynamics [14,17]. Previous research on ferns has mainly focused on selected temperate species, such as *Polystichum acrostichoides* and *Phyllitis scolopendrium*, or on a few tropical species, mostly tree ferns, leaving herbaceous ferns largely understudied [15,23,24]. The low mortality rates observed in this study may explain the lack of previous reports, as obtaining meaningful estimates requires monitoring large numbers of individuals over long periods of time. Although our study successfully followed over 3000 individuals, the two-year duration limits our ability to capture the effects of rare but significant mortality events, such as extreme climatic conditions, landslides, or other biotic factors.

The impact of temperature may be intensified by extreme climatic events, such as those associated with El Niño-Southern Oscillation (ENSO) cycles. Despite the rarity of such events in this region, they have been documented to influence mortality rates in other tropical systems by modifying water availability and increasing stress on plant communities [25–28]. However, these abiotic factors do not act in isolation. Landslides, which often interact with elevation-dependent factors to exacerbate fern mortality and are particularly prevalent in the Andean region, can physically remove individuals, destabilize substrates, and create competitive dynamics by altering light and nutrient availability [29]. Similarly, tree falls, another common disturbance, often create canopy gaps that alter microhabitats, potentially favoring species better adapted to higher light conditions [30]. On a regional scale, both types of disturbance are likely to influence significant fern mortality and community restructuring over time, even if they did not directly affect our study plots during the monitoring period.

Combined with the abiotic and climatic stressors discussed previously, the potential for increased herbivory under changing climate regimes may further exacerbate fern mortality. It has been demonstrated that herbivory on ferns can be considerable, with leaf area losses ranging from 7% to 20% in certain species [31]. Such damage can result in a reduction in photosynthetic capacity, a decline in reproductive success, and an increased susceptibility to pathogens, thereby increasing the risk of mortality. In addition, herbivory on reproductive structures such as sporangia can lead to a severe reduction in spore production, ultimately compromising population sustainability [32]. This vulnerability is further exacerbated by climatic changes, as experimental warming studies, such as that by Buckley (2023) [33], have shown that increased temperatures heighten the susceptibility of high-elevation plant populations to specialist herbivores. This suggests that ferns, particularly those in high-altitude habitats, may face compounded risks under warming scenarios, where elevated temperatures not only stress physiological processes but also amplify herbivore activity. Consequently, increased herbivore pressure represents a significant threat to fern populations, potentially leading to a notable decline in their abundance and distribution.

This interplay of abiotic and biotic factors highlights the complexity of fern population dynamics and underscores the need for long-term monitoring to fully capture the effects of both gradual environmental changes and acute disturbances.

The most striking result of our study is the remarkably low estimated mean annual mortality rate of 0.87%. This highlights the overall stability of fern populations within the study area. While our short-term estimates may exclude occasional massive mortality events, the low mortality rates observed could be linked to the unique life history traits of ferns. Specifically, their independent gametophytic stage likely contributes to prolonged generation times and reduces the need for frequent recruitment events [34]. Nonetheless, climate change poses a significant threat to this stability by intensifying disturbances such as prolonged droughts, extreme temperatures, or altered precipitation patterns [35,36]. These changes could increase physiological stress on ferns and amplify the frequency or severity of mortality events, potentially undermining the persistence of populations in the long term.

The observed relationship between fern mortality rates, elevation, and temperature showed a non-linear pattern, with mortality rates being highest at intermediate elevations and temperatures and decreasing at both extremes of the gradient. For example, at higher elevations (e.g., 3500 m asl) and temperatures, mortality rates approach 0%, while at intermediate elevations and temperatures, mortality rates peak. This pattern of mortality suggests that abiotic stress and biotic interactions such as herbivory (which has previously been discussed) and competition may vary across the gradient.

Another key result of our study is the observed relationship between mortality rates, species richness, and the density of fern individuals. Due to the covariance between these two factors, it remains unclear which has a greater influence on mortality patterns. Nevertheless, these findings also suggest that competition plays a role in structuring tropical fern assemblages. This insight is particularly intriguing because terrestrial ferns often grow scattered within tropical forests [30], with limited direct physical contact between individuals, making competitive interactions less apparent. However, a previous analysis of plant communities in temperate rainforests revealed a relationship between species richness and the functional diversity of leaf traits, indicating that competition for resources such as light and nutrients influences community structure [37]. All these studies, including ours, point to an important and poorly understood role of interspecific competition in structuring tropical fern assemblages.

Furthermore, our study shows a non-random distribution of mortality rates across size classes, with larger plants showing higher mortality rates compared to smaller individuals. This finding highlights the influence of size on mortality patterns in herbaceous plants, particularly tropical ferns. Larger individuals may be at increased risk due to their greater resource requirements and increased competition, particularly in areas of high plant density, such as the mid-elevations in our study area. Higher densities of individuals may increase competition for limited resources such as light and nutrients, further influencing size-dependent mortality rates. Previous research shows that size- and density-dependent effects significantly influence survival, with larger plants being more affected in denser communities [38]. Another study exhibited that functional traits like maximum height are key factors in shaping competitive interactions, as taller individuals may benefit from light acquisition but experience trade-offs such as heightened mortality due to resource constraints [39]. These findings highlight the importance of plant density and trait-mediated interactions in shaping mortality patterns and community dynamics across elevational gradients.

These last results emphasize the importance of considering plant size as a factor in demographic studies of ferns. Size-dependent mortality likely interacts with other ecological factors, such as competition, resource availability, and environmental disturbances, to shape fern population dynamics. Future research should investigate whether similar patterns occur across different environmental gradients and disturbance regimes to deepen our understanding of the demographic strategies and adaptive responses of tropical fern assemblages.

5. Conclusions

This study provides the first community-level estimates of tropical fern mortality, emphasizing the role of plant size, density, and environmental gradients. The remarkably low annual mortality rates observed, coupled with their non-linear relationship to elevation and temperature, highlight the overall stability of these populations under current conditions. However, the increased mortality at mid-elevations suggests that competition for limited resources, such as light and nutrients, plays a significant role in structuring fern assemblages. This underscores the importance of considering size-dependent mortality and its interactions with density and functional traits, such as maximum height, in understanding population dynamics.

Despite the stability observed, the potential for increased abiotic and biotic stressors, such as climate change, herbivory, and extreme climatic events, poses significant threats to fern populations. These factors may amplify mortality rates and disrupt community dynamics, particularly in high-density regions or areas prone to environmental disturbances. Long-term monitoring and expanded studies across diverse environmental gradients are crucial to fully capture the interplay of these factors and to anticipate how tropical fern populations may respond to future environmental changes.

Author Contributions: Conceptualization, L.S., M.K., J.K. and J.H.; methodology, L.S., M.K., J.K. and J.H.; investigation, L.S.; writing—original draft preparation, M.K. and L.S.; writing—review and editing, L.S., M.K., J.K. and J.H. All authors have read and agreed to the published version of the manuscript.

Funding: This research was funded by the Swiss National Science Foundation, grant number 0001711-188498.

Data Availability Statement: All the raw data used for the calculations presented in the figures and tables can be accessed in the Dryad Digital Repository [40].

Acknowledgments: We extend our deep appreciation to D. Torres, L. Cotugno, R. Güdel, E. Gortaire, W. Santillán, W. Pérez, and the members of the local communities for their invaluable assistance, support, and enthusiasm during the fieldwork. We also thank the Ministerio del Ambiente, Agua y Transición Ecológica of Ecuador (MAATE) for the institutional support and for granting the research permit Nº 09-IC-FAU/FLO-DPN/MA.

Conflicts of Interest: The authors declare no conflicts of interest. The funders had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript; or in the decision to publish the results.

References

1. Zhong, B.; Fong, R.; Collins, L.J.; McLenachan, P.A.; Penny, D. Two New Fern Chloroplasts and Decelerated Evolution Linked to the Long Generation Time in Tree Ferns. *Genome Biol. Evol.* **2014**, *6*, 1166–1173. [CrossRef]
2. Testo, W.L.; Sundue, M.A. Are Rates of Species Diversification and Body Size Evolution Coupled in the Ferns? *Am. J. Bot.* **2018**, *105*, 525–535. [CrossRef] [PubMed]
3. Page, C.N. Ecological Strategies in Fern Evolution: A Neopteridological Overview. *Rev. Palaeobot. Palynol.* **2002**, *119*, 1–33. [CrossRef]
4. Corlett, R.T.; Westcott, D.A. Will Plant Movements Keep up with Climate Change? *Trends Ecol. Evol.* **2013**, *28*, 482–488. [CrossRef] [PubMed]
5. Condit, R.; Ashton, P.; Bunyavejchewin, S.; Dattaraja, H.S.; Davies, S.; Esufali, S.; Ewango, C.; Foster, R.; Gunatilleke, I.A.U.N.; Gunatilleke, C.V.S.; et al. The Importance of Demographic Niches to Tree Diversity. *Science* **2006**, *313*, 98–101. [CrossRef]
6. Nepstad, D.C.; Tohver, I.M.; Ray, D.; Moutinho, P.; Cardinot, G. Mortality of Large Trees and Lianas Following Experimental Drought in an Amazon Forest. *Ecology* **2007**, *88*, 2259–2269. [CrossRef]
7. Laube, S.; Zotz, G. Long-term Changes of the Vascular Epiphyte Assemblage on the Palm Socratea Exorrhiza in a Lowland Forest in Panama. *J. Veg. Sci.* **2006**, *17*, 307–314. [CrossRef]
8. Marbà, N.; Duarte, C.M.; Agustí, S. Allometric Scaling of Plant Life History. *Proc. Natl. Acad. Sci. USA* **2007**, *104*, 15777–15780. [CrossRef]
9. Quarles, B.M.; Roach, D.A. Ageing in an Herbaceous Plant: Increases in Mortality and Decreases in Physiology and Seed Mass. *J. Ecol.* **2019**, *107*, 1409–1418. [CrossRef]
10. Hietz, P. Population Dynamics of Epiphytes in a Mexican Humid Montane Forest. *J. Ecol.* **1997**, *85*, 767. [CrossRef]
11. Oliva, J.; Stenlid, J.; Martínez-Vilalta, J. The Effect of Fungal Pathogens on the Water and Carbon Economy of Trees: Implications for Drought-Induced Mortality. *New Phytol.* **2014**, *203*, 1028–1035. [CrossRef] [PubMed]
12. Linares-Palomino, R.; Cardona, V.; Hennig, E.I.; Hensen, I.; Hoffmann, D.; Lendzion, J.; Soto, D.; Herzog, S.K.; Kessler, M. Non-Woody Life-Form Contribution to Vascular Plant Species Richness in a Tropical American Forest. *Plant Ecol.* **2009**, *201*, 87–99. [CrossRef]
13. Brock, J.M.R.; Perry, G.L.W.; Burkhardt, T.; Burns, B.R. Forest Seedling Community Response to Understorey Filtering by Tree Ferns. *J. Veg. Sci.* **2018**, *29*, 887–897. [CrossRef]
14. Mehltreter, K.; Walker, L.R.; Sharpe, J.M. *Fern Ecology*; Cambridge University Press: Cambridge, UK, 2010. [CrossRef]
15. Bucharová, A.; Münzbergová, Z.; Tájek, P. Population Biology of Two Rare Fern Species: Long Life and Long-Lasting Stability. *Am. J. Bot.* **2010**, *97*, 1260–1271. [CrossRef] [PubMed]
16. Sharpe, J. Growth, Demography, Tropic Responses and Apical Dominance in the Neotropical Fern Danaea Wendlandii Reichenb. (Marattiaceae). Ph.D. Thesis, University of Georgia, Athens, GA, USA, 1988.
17. Bystriakova, N.; Bader, M.; Coomes, D.A. Long-Term Tree Fern Dynamics Linked to Disturbance and Shade Tolerance. *J. Veg. Sci.* **2011**, *22*, 72–84. [CrossRef]
18. Kessler, M.; Salazar, L.; Homeier, J.; Kluge, J. Species Richness-Productivity Relationships of Tropical Terrestrial Ferns at Regional and Local Scales. *J. Ecol.* **2014**, *102*, 1623–1633. [CrossRef]
19. Legendre, P.; Fortin, M.J. Spatial Pattern and Ecological Analysis. *Vegetatio* **1989**, *80*, 107–138. [CrossRef]
20. Karger, D.N.; Kluge, J.; Abrahamczyk, S.; Salazar, L.; Homeier, J.; Lehnert, M.; Amoroso, V.B.; Kessler, M. Bryophyte Cover on Trees as Proxy for Air Humidity in the Tropics. *Ecol. Indic.* **2012**, *20*, 277–281. [CrossRef]
21. R Core Team. *R: A Language and Environment for Statistical Computing*; R Foundation for Statistical Computing: Vienna, Austria, 2022. Available online: https://cran.r-project.org/doc/manuals/r-release/fullrefman.pdf (accessed on 27 November 2024).
22. Wickham, H. ggplot2: Elegant Graphics for Data Analysis. 2009. Available online: https://ggplot2-book.org/ (accessed on 27 November 2024).
23. Kuehn, D.M.C.; Leopold, D.J. Long-Term Demography of *Phyllitis scolopendrium* (L.) Newm. Var. Americana Fern. in Central New York. *Bull. Torrey Bot. Club* **1992**, *119*, 65. [CrossRef]
24. Greer, G.K.; McCarthy, B.C. Patterns of Growth and Reproduction in a Natural Population of the Fern Polystichum Acrostichoides. *Am. Fern J.* **2000**, *90*, 60. [CrossRef]
25. Olivares, I.; Svenning, J.C.; van Bodegom, P.M.; Valencia, R.; Balslev, H. Stability in a Changing World—Palm Community Dynamics in the Hyperdiverse Western Amazon over 17 Years. *Glob. Chang. Biol.* **2017**, *23*, 1232–1239. [CrossRef] [PubMed]
26. Griffin-Nolan, R.J.; Mohanbabu, N.; Araldi-Brondolo, S.; Ebert, A.R.; LeVonne, J.; Lumbsden-Pinto, J.I.; Roden, H.; Stark, J.R.; Tourville, J.; Becklin, K.M.; et al. Friend or Foe? The Role of Biotic Agents in Drought-Induced Plant Mortality. *Plant Ecol.* **2021**, *222*, 537–548. [CrossRef]
27. Corlett, R.T. Impacts of Warming on Tropical Lowland Rainforests. *Trends Ecol. Evol.* **2011**, *26*, 606–613. [CrossRef] [PubMed]
28. Browne, L.; Markesteijn, L.; Engelbrecht, B.M.J.; Jones, F.A.; Lewis, O.T.; Manzané-Pinzón, E.; Wright, S.J.; Comita, L.S. Increased Mortality of Tropical Tree Seedlings during the Extreme 2015–16 El Niño. *Glob. Chang. Biol.* **2021**, *27*, 5043–5053. [CrossRef]
29. Walker, L.R.; Shiels, A.B. *Landslide Ecology*; Cambridge University Press: Cambridge, UK, 2010. [CrossRef]
30. Poulsen, A.D.; Nielsen, I.H. How Many Ferns Are There in One Hectare of Tropical Rain Forest? *Am. Fern J.* **1995**, *85*, 29. [CrossRef]

31. Winkler, M.; Hülber, K.; Mehltreter, K.; Franco, J.G.; Hietz, P. Herbivory in Epiphytic Bromeliads, Orchids and Ferns in a Mexican Montane Forest. *J. Trop. Ecol.* **2005**, *21*, 147–154. [CrossRef]
32. Mesipuu, M.; Shefferson, R.P.; Kull, T. Weather and Herbivores Influence Fertility in the Endangered Fern Botrychium Multifidum (S.G. Gmel.) Rupr. *Plant Ecol.* **2009**, *203*, 23–31. [CrossRef]
33. Buckley, J.; Widmer, A.; Mescher, M.C.; De Moraes, C.M. Experimental Warming Increases the Vulnerability of High-Elevation Plant Populations to a Specialist Herbivore. *Funct. Ecol.* **2023**, *37*, 1536–1552. [CrossRef]
34. Watkins, J.E.; Cardelús, C.L. Ferns in an Angiosperm World: Cretaceous Radiation into the Epiphytic Niche and Diversification on the Forest Floor. *Int. J. Plant Sci.* **2012**, *173*, 695–710. [CrossRef]
35. Pouteau, R.; Meyer, J.Y.; Blanchard, P.; Nitta, J.H.; Terorotua, M.; Taputuarai, R. Fern Species Richness and Abundance Are Indicators of Climate Change on High-Elevation Islands: Evidence from an Elevational Gradient on Tahiti (French Polynesia). *Clim. Chang.* **2016**, *138*, 143–156. [CrossRef]
36. Pie, M.R.; Batke, S.P.; Reyes-Chávez, J.; Dallimore, T. Fern and Lycophyte Niche Displacement under Predicted Climate Change in Honduras. *Plant Ecol.* **2022**, *223*, 613–625. [CrossRef]
37. Saldaña, A. Relación Entre Riqueza de Especies y Diversidad Funcional de Atributos Foliares En Dos Ensambles de Especies Siempreverdes de Un Bosque Templado Lluvioso. *Gayana Bot.* **2013**, *70*, 177–187. [CrossRef]
38. Schamp, B.S.; Aarssen, L.W. Plant Species Size and Density-Dependent Effects on Growth and Survival. *J. Veg. Sci.* **2014**, *25*, 657–667. [CrossRef]
39. Long, W.; Schamp, B.S.; Zang, R.; Ding, Y.; Huang, Y.; Xiang, Y. Community Assembly in a Tropical Cloud Forest Related to Specific Leaf Area and Maximum Species Height. *J. Veg. Sci.* **2015**, *26*, 513–523. [CrossRef]
40. Kessler, M.; Salazar, L.; Homeier, J.; Kluge, J. Data from: Species Richness–Productivity Relationships of Tropical Terrestrial Ferns at Regional and Local Scales. *Dryad Digit. Repos.* **2014**, *102*, 1623–1633. [CrossRef]