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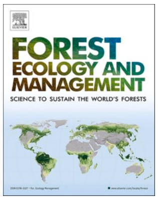

Seedling emergence and environmental filters determine *Ficus* recruitment in a subtropical landscape

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ABSTRACT

Early regeneration, involving the transition from a seed into a successfully recruited seedling, is a complex process characterized by high mortality rates and the strong association with environmental filters. However, we have limited understanding of the factors and transitional regeneration stages that lead to these broad mortality events, even in species that are key for ecosystem function and comprise the bulk of species in diversity assessments, such as *Ficus* species. Using eight, 1-ha long term monitoring plots, established along an elevation gradient in tropical to subtropical forests in southern China, and partitioning the early plant regeneration process into four stages (seed germination, seedling emergence, establishment and recruitment), we conducted a seed addition experiment to assess the factors driving the early regeneration process. We used four hemi-epiphytic and four non-hemiepiphytic *Ficus* species, specifically asking whether elevation, microsite conditions and growth form affect the success of regeneration outcomes. We observed that *Ficus* early regeneration was highly limited throughout the subtropical landscape with similar seed germination probabilities along all elevations, but greater seedling emergence at higher elevations. Growth form and elevation interacted significantly during seed germination and seedling emergence stages. The strongest filtering effect was observed during seedling emergence, with greater canopy openness facilitating, but drier and cooler soils being less conducive to seedling emergence, especially for hemiepiphytic species. Once emerged, *Ficus* seedlings were released from the environmental filters assessed here, yet, continued to face successively greater mortality during establishment and recruitment. Greater seed germination and seedling emergence on the ground observed in hemiepiphytes indicate that they may benefit from evolutionary traits associated with canopy regeneration under water and temperature stress, but only at the early regeneration stages, as seedling establishment and recruitment were similar in both groups. In general, our results demonstrate that even when seeds are available, successful recruitment is strongly limited by microsite conditions and growth form, through filtering mechanisms associated with the transition from seedling emergence to seedling establishment. The identification of environmental filters that operate during the complex and vulnerable early regeneration stages provides a baseline to develop management strategies for *ex situ* conservation, as well as *in situ* population reestablishment for restoration.

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1. Introduction

Early plant regeneration, which is characterized by high mortality, plays a central role in influencing key ecological processes, including population dynamics, species diversity, community assembly and ecosystem function (Fenner, 1985). At each stage of plant regeneration, the developing propagule undergoes rapid internal biophysiological change, while interacting with environmental filters, levied by biotic and abiotic factors (Benavides et al., 2016; Eriksson and Ehrlén, 2008; Fenner, 1985; Larson et al., 2015; Muller-Landau et al., 2002). The extent to which environmental filters interact and impact successful transition through each regeneration stage, has cascading effects on the major drivers of biodiversity change, habitat fragmentation, overharvesting, biological invasions and climate change, unleashing alterations in species abundance, composition and diversity (Walck et al., 2011).

Despite the critical role environmental filters play in determining early plant regeneration, we still lack an empirical understanding of which factors and which transitional stages lead to the broad mortality events common during early regeneration (Larson et al., 2015). To date, experimental studies focusing on the effect of environmental filters in determining early regeneration success have found both biotic (predation, diseases and competition) and abiotic (drought, flooding, light, humidity, nutrients, temperature, and altitudinal variation) determining as constraining factors, mainly operating during seed germination and seedling emergence (Clarke and Davison, 2004; Fenner, 1985; Grubb, 1977; Khan and Gulzar, 2003; Larson et al., 2015; Myster, 2017; Wright et al., 1998). A few studies have postulated the factors that determine regeneration success and the most sensitive early regeneration stage. For example, Larson et al. (2015) identified that regardless of soil moisture, seed germination and seedling emergence probabilities explained 90% of the variation in recruitment of 47 dryland grasses, with emergence being the strongest predictor of cumulative survival. Wright et al. (1998), assessed seedling emergence and survival in six forest tree species and showed that gap position and seedbed substrate were most influential on these two regeneration stages, with diminished influence from substrate as regeneration progressed. Clarke and Davison (2004) found differences in herbaceous seedling emergence and survival related to ground cover heterogeneity, soil surfaces and herbivory.

Environmental variation caused by altitude can significantly alter the regeneration process through cascading and complex interactions (Giménez-Benavides et al., 2007; Mariko et al., 1993). The altitudinal effects on the regeneration process can be attributed to significant changes in the photothermal environment. Benavides et al. (2016) identified significant interactions between annual mean temperature and local factors such as light availability, stand structure and ground cover, implying that climate and local heterogeneity conditions may mitigate or aggravate the effect of climate on juveniles. Local climate of elevation gradients has also strong effects on tree size, tree maturity, growth rate, predation and tree mortality elucidating future changes in forest distribution and structure as a result of changes in climate and biotic interactions (Gworek et al., 2007).

Elevation gradients and surrounding factors mediate seed and seedling performance through intraspecific trait variations. For example, Gworek et al. (2007) found at middle and high elevations more filled seeds in pine cones and greater pine seedling survival. Dorne (1981) showed that at altitudes, *Chenopodium bonus-henricus* achenes have thicker seed coats and higher polyphenol contents reducing permeability of the seed coat and O_2 flux to the seed embryo resulting in lower germination. It is hypothesized that the increase in polyphenol content is due to increases in visible radiation and decreases in temperatures. Furthermore, altitude determines the distribution of pollinators (Giménez-Benavides et al., 2007), dispersal agents (Levey, 1988; McConkey et al., 2012) and tolerance of seed and seedlings to environmental conditions that change with altitude, especially temperature (Jump and Woodward, 2003; Sharma and Kala, 2018). Altitude variations imposed by mountainous regions can also be an important factor for dispersal processes, which can impede the passage of migratory seed-eating or fruit-eating birds (Fenner, 1985; Fenner and Thompson, 2005). Likewise, at the edges of altitudinal ranges and beyond them, seed availability and the appropriate microsites for germination can also limit recruitment (Kroiss and HilleRisLambers, 2015; Münzbergová and Herben, 2005).

The limitations operating on the early regeneration transition from seed to seedling are difficult to characterize and quantify, especially under field conditions (Clark et al., 1998; Kroiss and HilleRisLambers, 2015; Larson et al., 2015; Valdez et al., 2019). An adequate understanding of limitations imposed on plant regeneration at each successive stage, gained through empirical field-based studies, could guide niche-based species selection (Ribbens et al., 1994) and help define the main environmental filters that modulate species performance and community assembly in forest management applications (Keddy, 1992; Larson et al., 2015; Münzbergová and Herben, 2005; Statton et al., 2017; Werden et al., 2020). However, such comprehensive studies that investigate early plant regeneration limitation in the field are time consuming and rare making necessary to focus on each stage of the regeneration process (Wenny, 2000).

Assessing the relative influence of environmental filters and determining the critical early regeneration stages that shape recruitment is a key requirement for building trait-based predictions for plant demographic processes (Statton et al., 2017). For each environmental filter acting during the regeneration process, some species may exhibit functional traits necessary to pass through the filter or have traits that are more responsive, which would allow them to overcome the limitation, increasing their comparative abundance (Hallett, 2010; Keddy, 1992). The variation in response to environmental filters during regeneration could be considered as the result of strong evolutionary forces that allow species to develop new morphological and physiological attributes and overcome ecological limitations (Chen et al., 2021; Hao et al., 2013; Ji et al., 2018), resulting in a wider range of habitats for diversification among a wide range of taxa (Watts et al., 2019; Zhang et al., 2015). For example, *Ficus* hemiepiphytic species have accrued adaptive traits when compared to non-hemiepiphytic species that allow them to overcome selective forces exerted through environmental filtering in the canopy environment, such as drought and temperature stress (Chen et al., 2021; Hao et al., 2013, 2010) and soil nutrient deficiency (Schmidt and Tracey, 2006). Hemiepiphytes include both an epiphytic and a terrestrial phase during their life cycle while non-hemiepiphytes just include a terrestrial phase (Berg and Corner, 2005). There are two distinct patterns of hemiepiphytic growth; primary hemiepiphytes transition from regenerating as epiphytes to terrestrial growth by sending aerial roots to the ground and, secondary hemiepiphytes, which begin with terrestrial regeneration and later lose their rooting contact with ground (Berg and Corner, 2005; Putz and Holbrook, 1986). Although Zotz et al. (2021) in their review of hemiepiphyte biology argue that secondary hemiepiphytes should not be considered hemiepiphytes. Their growth form is better understood to be a climber that secondarily loses its root connection with the soil.

The epiphytic regeneration stage benefits from the nutrient-rich humus on host microsites and greater access to light, while escaping terrestrial herbivores, and ground-based hazards, such as flooding and ground fires (Laman, 1995; Putz and Holbrook, 1986; Williams-Linera and Lawton, 1995; Zotz et al., 2021). Water and light availability may interact differently on *Ficus* hemiepiphytic seedling adaptations showing a strong positive response to light level when water is abundant (Laman, 1995; Swagel et al., 1997). However, in the transient canopy conditions, regenerating seedlings may be exposed to other perils, including drought, excessive irradiance and heat that can quickly desiccate and damage germinating seeds and emerging seedlings (Harrison, 2006; Laman, 1996; Putz and Holbrook, 1986). Yet, we lack empirical, spatially extensive, and field-based comparative studies to determine the effect of environmental filters on the early regeneration process that could explain the divergence in growth form.

Suitable candidates to assess the effects of environmental filtering on plant regeneration might be groups of species with strong effects on communities and ecosystems, a variety of ecological attributes that when removing the species effects in the local biodiversity are significant, and reproduction at low densities. Such species could provide critical insights into factors that limit regeneration. Keystone species (Mills et al., 1993; Paine, 1969) meet these characteristics (Power et al., 1996). They have a relatively low abundance compared to their influence on the ecosystem (Power et al., 1996) and their loss could cause a disproportionately large effect on communities as they fulfill important functions in biological and ecological interactions (Harrison, 2003; Mills et al., 1993; Sreekar et al., 2010). Members of the genus *Ficus*, commonly known as figs (family Moraceae), are often regarded as keystone species. They have a specialized pollination system, high year-around fruit production and they strongly impact the abundance, distribution and behavior of large frugivores (e.g., Harrison, 2003; Kinnaird and O'brien., 2005; Peabotuwage et al., 2019). Figs also exhibit a high diversity of life forms, including species that are vines, shrubs, epiphytes, hemiepiphytes and terrestrial woody trees, which allows them to colonize microsites varying from the understory to canopy emergent layers (Berg and Corner, 2005; Harrison, 2005a). Although figs have numerous species that co-occur and are primary components in diversity assessments of tropical landscapes (Harrison, 2005b), they are typically rare, especially the monoecious hemiepiphytic figs, in natural forests (Harrison, 2005b; Harrison et al., 2003). This is attributed to their specialized microsite requirements for regeneration and their very divergent niches, which are rare in primary forests (Harrison, 2005a) and significantly limit recruitment opportunities (Laman, 1995). Figs are recruitment limited despite possessing strategies such as, small seed size and high fecundity, which are essential for securing infrequent and widespread recruitment opportunities (Harrison, 2005a; Jakobsson and Eriksson, 2000). This indicates potential limitations in the early regeneration process in *Ficus* species. The primary hemiepiphytic *Ficus* species, hereafter referred to as hemiepiphytes, and terrestrial *Ficus* species contrast in their plant life starts but both have terrestrial adult habit. Thus, they are suitable candidates to assess how environmental filters operate on these contrasting regeneration strategies.

Many studies on figs have focused on their highly specialized reproductive system (Cook and Rasplus, 2003) and strong ecological interactions with seed dispersers (Compton et al., 1996; Kirika et al., 2008; Lambert and Marshall, 1991; Shanahan et al., 2001) and a few provide a detailed understanding of their regeneration ecology (Banack et al., 2002; De Figueiredo et al., 1995; Harrison, 2006; Laman, 1996; Lin et al., 2008). Banack et al. (2002) found that *Ficus* species seem to be more establishment limited than dispersal limited. However, studies have shown a mismatch between seed deposition and seedling establishment microhabitats; *Ficus* seedlings are often found in open areas (roadside, canopy gaps and forest edge), while seeds are usually deposited beneath the closed canopy (e.g., Zhou and Chen, 2010). Thus, optimal deposition of seeds in suitable microsites, which increases survivorship, may also be important for regeneration success in *Ficus* (Banack et al., 2002; De Figueiredo, 1993; Laman, 1995). Studies on *Ficus* seed germination and seedling recruitment in natural conditions have shown a high mortality of individuals (Harrison, 2006; Laman, 1995) and in laboratory conditions, high germination but low recruitment occurs (Chen et al., 2021). Therefore, as practitioners of forest restoration and conservation we ask, what happens in natural environments between the seed germination stage and the final *Ficus* seedling recruitment? Is there a bottleneck between these stages that does not allow the seedling to transition from one stage to the other? Discordances between seed arrival, seed germination and establishment limitations could explain higher endemism and vulnerability to disturbance and fragmentation (Harrison, 2003), target management and restoration practices important to maintain *Ficus* populations under rapidly changing climate regimes and call for empirical studies that investigate regeneration process in detail.

Species demographic and ecophysiological studies are important tools for the generation of techniques and strategies for forest management, restoration and conservation. These studies allow us to understand the behavior and availability of propagules, the probabilities of transition from one early regeneration stage to another, and the biotic and abiotic variables that determine the probabilities of a seed becoming an autotrophic plant that contributes to the assembly of a functional ecosystem (Lu et al., 2016; Martínez-Ramos et al., 2016). Understanding the mechanisms around the early plant regeneration is a fundamental factor for forest management since it allows determining the possibilities of use, in production, conservation or regulation.

In this study, using a network of eight 1-ha plots established for monitoring long-term forest dynamics in subtropical China, we assessed the influence of six environmental filters on the stages that compose the early plant regeneration process in hemiepiphytic and non-hemiepiphytic *Ficus* species using a seed addition experiment. Specifically, we hypothesized that each regeneration stage is influenced by microclimatic factors (canopy openness, soil temperature, soil moisture and soil pH) and elevation as well as species biology, specifically by growth form, as each seed-to-seedling stage might have different biotic and abiotic requirements to overcome one regeneration stage to other. We predicted that regardless of growth habit, *Ficus* species will experience environmental barriers imposed by changes in elevation while transitioning through each early regeneration stage, but that seed germination will be the least limiting stage (Chen et al., 2021, 2013; De Figueiredo et al., 1995). We also expected that the environmental factors operating on each regeneration stage would be characteristic to the specific stage, with establishment and recruitment being the most sensitive as the transition to become an autotrophic seedling requires independence of seed storage resources and faces more environmental barriers (Baskin and Baskin, 2014; Harrison et al., 2003; Laman, 1995). Given that hemiepiphytic growth form is considered as an adaptation to overcome low light conditions in the forest understory (Harrison et al., 2003), and because most fig species' germination is promoted by light (Berg and Corner, 2005; Laman, 1995), canopy openness is likely to be one of the most influential factors in determining germination and other factors to have greater effects on later regeneration stages (Fu et al., 2008; Zhou and Chen, 2010). Climatic conditions change rapidly along altitudinal gradients, which in turn can influence regeneration processes (Kroiss and HilleRisLambers, 2015). Thus, we expect there to be lesser limitations on the early regeneration process of both growth forms, at low elevations, where warm temperature and low relative humidity prevail. Finally, as this study is carried out on the forest floor, we expect that non-hemiepiphytic species will be less limited during the early regeneration process compared to hemiepiphytic species, whose regeneration niche is in the forest canopy.

2. Materials and methods

2.1. Study sites description

We conducted this study within the Sino-Himalayan subtropical forest biome (BirdLife International, 2009), in four National Nature Reserves in Guangxi Zhuang Autonomous Region, Southern China (Appendix S2: Fig. S1): Cenwanglaoshan (CWL; 24°21′ N, 106°27′ E; broadleaf evergreen forest), Dayaoshan (DYS; 23°52′ N, 110°01′ E; broadleaf evergreen forest), Mulun (ML; 25°07′ N, 107°54′ E; karst landscape with subtropical mixed evergreen deciduous broadleaf forest), and Damingshan (DMS; 23°28′ N, 108°23′ E; subtropical monsoon evergreen broadleaf forests). We selected eight 1-ha plots (two plots from each reserve), established in relatively undisturbed locations, which belong to the long-term forest dynamics monitoring plot network administered by the College of Forestry, Guangxi University. Our plots span an elevation range from 400 m. a.s.l to 1850 m. a.s.l. (further information on site and plot characteristics is found in Appendix S2:

Table S1; Appendix S2: Fig. S1).

2.2. Study species and seed collection

Our study design included four hemiepiphytic (H: *Ficus benjamina, F. concinna, F. microcarpa and F. tinctoria*) and four non-hemiepiphytic (NH: *F. auriculata, F. oligodon, F. racemosa* and *F. semicordata*) fig species naturally occurring in Guangxi within our study sites. We have selected representative hemiepiphytic species from both subgenera, *Urostigma* (three species) and *Sycidium* (one species) in which hemiepiphytes occur in the genus *Ficus* (Cruaud et al., 2012). The non-hemiepiphytes mainly appear in five subgenera contained in three system branches, and our species are representative of two subgenera contained in one system branch (Cruaud et al., 2012; Appendix S2: Table S2). We randomly collected fresh mature syconia (i.e., fruits) from a minimum of five trees for each species in Yunnan and Guangxi provinces during 2018 and 2019. Seeds were manually extracted, cleaned using water and sieved to remove the pulp. During the washing process, empty seeds that floated were discarded. Later, seeds were air dried for a day and transferred to the Regeneration Ecology, Seed Biophysiology and Conservation Laboratory at Guangxi University for storage at 10 °C in paper bags. Prior to experimentation, we verified seed viability using laboratory germination tests following protocols implemented by Chen et al. (2021). Seeds from seed lots with $>$ 98% viability were used for the following experiment conducted between July 2019 and November 2019.

2.3. Experimental design

Surrounding and at 5 m from the perimeter of each 1-ha plot, at each of the selected eight elevations, we established three replicates of gap (G) and three replicates of non-gap (NG) microsite positions (total of six microsite positions at each elevation), a variable considered important for *Ficus* colonization (Fu et al., 2008; Hao et al., 2013; Vázquez-Yanes et al., 1996) to monitor limitations of the early regeneration stages (ERS) of *Ficus* species (total: 2 microsites * 3 replicates for each microsite * 8 elevations = 48 microsites; Fig. 1). The gap microsite was defined as places with canopy openness (CO; the percentage of light available observed in the different sections of a spherical densitometer) varying between 30 and 55% and non-gap microsite was identified as a place with CO varying between 5 and 30% as measured by a hand-held densiometer (Forestry Suppliers Inc., USA). The gap and non-gap categorization were based on the reconnaissance survey of the four forest reserves conducted six months prior to experiment and based on CO values for the regional subtropical forests (Martini et al., 2020). At a given elevation, microsite positions were placed $>$ 10 m from one another.

In each microsite, we implemented a seed addition experiment to identify factors governing the early regeneration stages from seed germination to seedling recruitment of *Ficus* using mesh size 60 nylon bags (60 fiber per inch; further specifications of the bag are in Appendix S1), hereafter referred to as “seed bags”, which were selected based on experimental testing to determine the best mesh size to securely contain the seeds under the experimental conditions without loss but also allow water and light penetration and successful seedling emergence and development (further details are in Appendix S1). In each seed bag we placed 20 seeds of each species, and positioned four seed bags (four replicates) in each microsite in an experimental 0.49 m^2 quadrat under a 0.5 cm soil layer. Before the placement of the experiment the forest floor surface was cleared of surface debris and delimited by 1-inch 70 * 70 cm PVC poles secured to the ground using metal hooks (Fig. 1). In order to measure whether seed arrival and subsequent recruitment occurs outside of the experimental placement of seeds, in each microsite position we established a control quadrat. Only 91 seedlings were identified as new recruits during the entire experimental period in control quadrats, but these were not definitively confirmed as belonging to the *Ficus* species studied here, and hence were not included in any analyses. Thus, our experimental design comprised of 48 experimental quadrats containing 1536 seed bags totaling 30,720 seeds (48 microsites * 8 species * 4 replicate seed bags for each species * 20 seeds in each seed bag; Appendix S2: Fig. S2). The seed bags were placed in June 2019 (summer) before the start of the rainy season. They were carefully opened and monitored first in August 2019 and again in November 2019 (autumn) in the middle of the dry season. The experiment is ongoing to as a long-term study and hence the final viability of seeds were not determined.

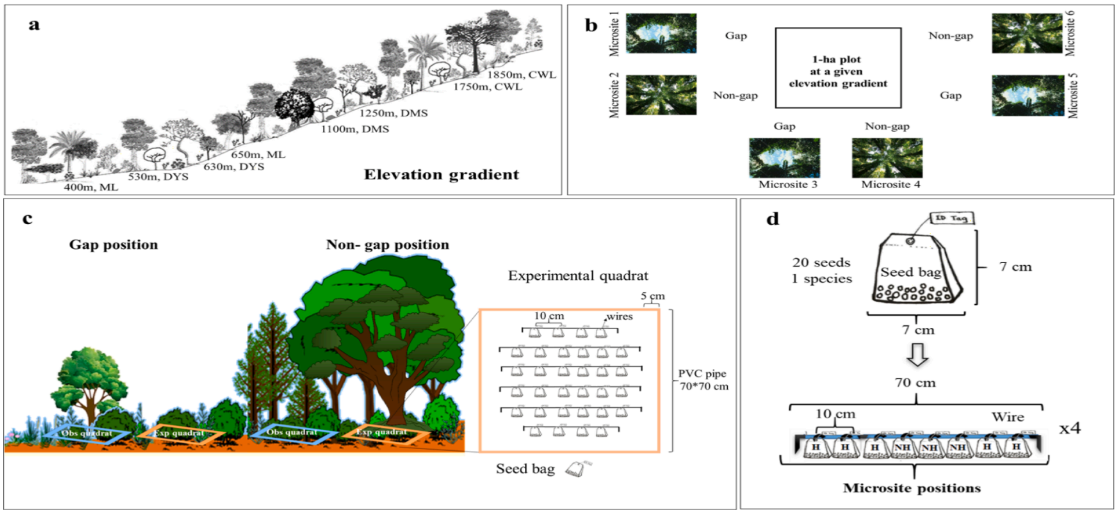

Fig. 1. Experimental design for the assessment of early regeneration stages of eight *Ficus* species using (a) an elevation gradient (400 m a.s.l. – 1850 m a.s.l.) comprising four subtropical forests in Guangxi province, South China (ML: Mulun, DYS: Dayaoshan, DMS: Damingshan, CWL: Cenwanglaoshan) and two 1-ha plots in each forest. (b) Each 1-ha plot contains six microsites that correspond to a gap and a non-gap position with three replicates each. (c) At each microsite, we installed, at 50 cm apart from each other, an observational (in blue) and an experimental (in orange) quadrant using 70 * 70 cm, polyvinyl chloride pipes. Each experimental quadrat contains a seed addition experiment and the observational quadrats were used as controls. (d) The seed addition experiment consisted of the use of 7*7 cm nylon bags which contained 20 seeds of the same species (either hemiepiphytic: H, or non-hemiepiphytic: NH). The bags were randomly located 10 cm apart each within the experimental quadrant using cables to tie them to the ground. Each quadrant had 32 bags (8 species * 4 replicates each). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2.4. Assessment of microsite environmental conditions

Before placing the experiment and at each census, we measured six microsite environmental factors in each gap (G) and non-gap (NG) position (Appendix S2: Table S1) four times a day from 8.00 h to 16.00 h: (1) CO to confirm our previous G and NG assignment for each microsite (2) soil pH measured using a regular soil pH-meter (AMTAST AMT-300, Shenzhen, Guangdong, China), (3) soil temperature and (4) soil moisture quantified using a dual soil temperature and moisture meter (L99-TWS-2, Hang Zhou Loggertech Co., Ltd., Hang Zhou, Zherjiang, China), (5) relative air humidity and (6) environmental temperature assessed using a thermo hygrometer (AR837 – Smart Sensor, ARCO Science & Technology Ltd., Guangzhou, Guangdong, China).

2.5. Early regeneration stages

Each ecological process represents a series of stages. Each stage is determined by different factors to finally fail or transition from one stage to another. In the case of the early plant regeneration, it begins with seed germination, followed by seedling establishment, identified as the shift from an emerged seedling to an autotrophic juvenile plant (Baskin and Baskin, 2014; Larson et al., 2015) and finally, established seedlings that have survived and persisted through the first growing season are usually considered recruits (Eriksson and Ehrlén, 2008; Zeiter et al., 2006). The early plant regeneration is considered as the most sensitive period in the plant history. The development of seedling autotrophy is gradual and it is considered as a young plant when is dependent on the food reserves stored in the seed. Once dependence is transferred to external sources, the plant can be considered to have passed the seedling stage (Kitajima and Fenner, 2000).

Based on pre-experiments on *Ficus* seedling growth conducted during this study in greenhouse and laboratory, and previous studies (Chen et al., 2021), we identified marked morphological (radicle, cotyledon and true leaves development) and physiological (drought tolerance) changes, which contributed to partition the early plant regeneration hereafter referred to as "Early Regeneration Stages (ERSs)" into four stages: seed germination (SGer), seedling emergence (SEmer) to seedling establishment (SEstab) and seedling recruitment (SREc) when the final hurdle in the process of plant regeneration happens (Fenner and Thompson, 2005).

At the end of the experiment, we measured whether the seeds in each tagged seed bag have failed or succeeded to achieve and pass each of the four ERSs by opening and assessing the seed bags using small scissor without disturbing any seedlings that were protruding out of the mesh surface. We counted each ERS as follows: SGer: number of seeds that germinated if 1 mm radicle emergence through the seed coat was observed; SEmer: number of seedlings that showed an elongated hypocotyl; SEstab: number of seedlings that had fully expanded cotyledons; and SRec: number of seedlings that had fully expanded true leaves. For each stage, we counted the total number of individuals that survived in each stage and calculated the probability of seed germination (SGer), seedling emergence (SEmer), seedling establishment (SEstab) and seedling recruitment (SRec) based on the number of seeds placed in the bags initially.

2.6. Modelling the early regeneration stages

All statistical analyses and figures were developed using R statistical software (version 4.1.0, R Core, 2021). We used generalized mixed-effects models (GLMMs) to determine how seed germination, seedling emergence, seedling establishment and seedling recruitment are governed in the subtropical landscape by elevation (from 400 m a.s.l. to 1850 m a.s.l.), growth form (hemiepiphytic versus non-hemiepiphytic), microsite position (gap versus non-gap), soil temperature, soil moisture and soil pH. We used species and site as a random effect (8 levels each) to control for species and site-level variation between the different factor levels. When species or site explained little variance and its removal improved the results (lower AIC), we did not keep it in the model. We standardized continuous predictors to facilitate the analysis.

We used binary response variables to predict the probability of each ERS from 0 to 1, where 0 is when failed to reach or pass the ERS and 1 when reached or passed the ERS. We calculated the binary response for each ERS probability using the *cbind* function in R. For all probability response variables, we checked all possible interactions among predictors, we verified collinearity (variance inflation factor – VIF < 3) using the *car* package (Fox and Weisberg, 2019) removing the factors that did not meet the VIF criteria, and we tested for spatial autocorrelation by performing the Moran.I test using the *DHARMa* package (Hartig, 2020). We checked overdispersion using *DHARMa* nonparametric dispersion test via standard deviation of fitted residuals vs. simulated data ($P > 0.05$) and we assessed the best-fit model for each ERS among the binomial and the Betabinomial models (glmmTMB package; Harrison, 2015) using the Akaike's information criterion values (MuMIn package; Barton, 2019). The Binomial aggregated regression best fitted for seedling emergence (SEmer) and seedling recruitment (SRec) probability response variables. The Beta-Binomial model, which employs a Template Model Builder (Brooks et al., 2017) to account for overdispersed binomial data, a common characteristic of biological data models (Harrison, 2015), was the best fit to seed germination (SGer) and seedling establishment (SEstab) probability response variables. Each full model had the following form:

$$Y\ \beta_0 + \beta_1 Gf + \beta_2 Ele + \beta_3 Mp + \beta_3 St + \beta_3 Sm + \beta_3 SpH + \beta_4 Int + \varepsilon_{sp} + \varepsilon_s + \varepsilon_{residual}$$

where *Y* is the probability response variable for each ERS (SGer, SEmer, SEstab, SRec), *Gf* is the species' growth form (hemiepiphytic or non-hemiepiphytic), *Ele* is the elevation, *Mp* is the microsite position (gap or non-gap), *St* is the soil temperature, *Sm* is the soil moisture, *SpH* is the soil pH and *Int* is the interaction. Species and site as random factors are denoted by ε_{sp} and ε_{s} respectively and $\varepsilon_{\text{residual}}$ is the residual error (further details are in Appendix S2: Table S3). As we cannot compare each ERS due to their dependence, we determined the stronger filter of the early regeneration process based on the number of factors significantly affecting each stage. The greater number of significant factors, the greater barriers imposed by the environment to overcome each ERS, threatening the seed-to-seedling success transition. Mean and standard error values are presented when reporting results.

3. Results

Out of the 30,720 seeds placed in seed bags across the subtropical forest landscape, 9,766 *Ficus* seeds germinated (31.8% ± 0.7), 996 seedlings emerged (3.24% ± 0.22), 104 seedlings were established (0.33% ± 0.04) and 21 seedlings were recruited (0.06% ± 0.001). Hemiepiphytic species registered higher percentage values during the first three ERSs (SGer = 41.86% ± 2.11, SEmer = 5.24% ± 0.76, SEstab = 0.38 ± 0.12, SRec = 0.06 ± 0.04) when compared with non-hemiepiphytic species (SGer = 21.72% ± 1.38, SEmer = 1.24% ± 0.35, SEstab = 0.29 ± 0.11, SRec = 0.08 ± 0.05; Appendix S2: Fig. S2). In general, the probability response of the ERS was significantly different from each other decreasing as the early regeneration process moves forward ($P < 0.05$; Fig. 2).

3.1. Seed germination (SGer)

This stage presented the highest mean percentage values (Fig. 2), and growth form, microsite position and the interaction between growth form and elevation were the driver factors of seed germination probability among eight *Ficus* species at landscape level when having species and site as random effects ($R^2m = 0.183$, $R^2m = 0.170$; $R^2c = 0.282$, $R^2c = 0.262$; Appendix S2: Table S3; Fig. 3); at gap microsite positions, germination probability was higher (0.35 ± 0.004) compared to non-gap

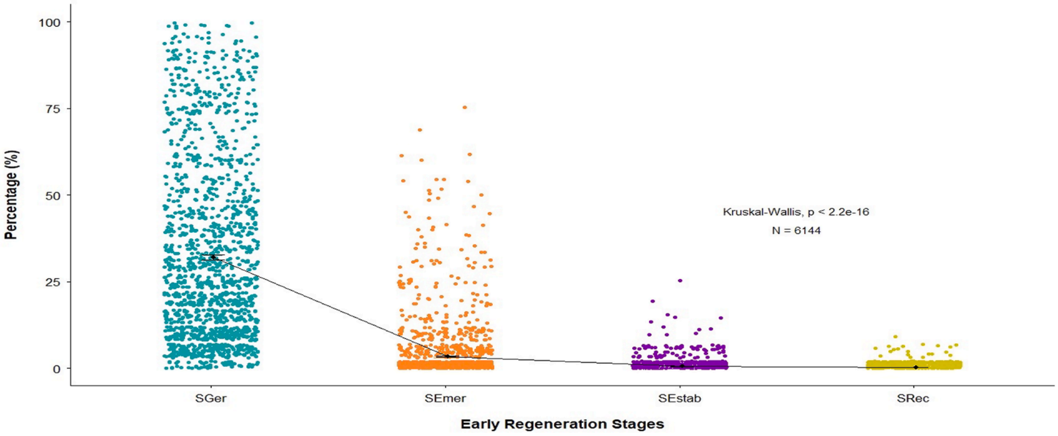

Fig. 2. Boxplot of percentage data distribution among the early regeneration stages (ERS): seed germination (SGer), seedling emergence (SEmer), seedling establishment (SEstab), seedling recruitment (SRec). Kruskal-Wallis test value and sample size (N = 1536 bags * 4 ERS) are shown.

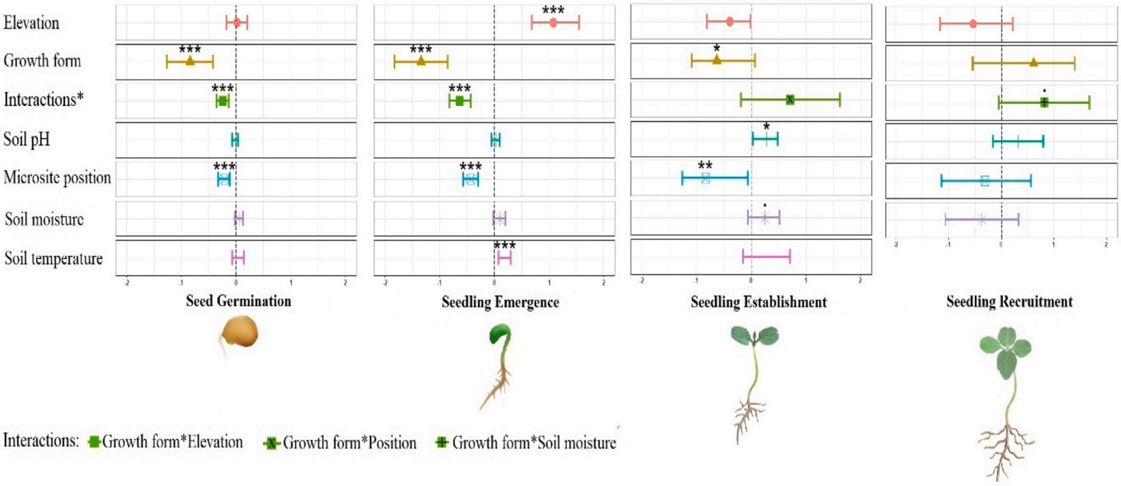

Fig. 3. Estimated full coefficients and 95% confidence intervals for the effects of elevation, growth form, soil temperature, soil pH, microsite position, soil moisture, and the interactions between growth form and elevation, position and soil moisture on the probability of the early regeneration stages: seed germination, seedling emergence, seedling establishment, seedling recruitment. *P* values are shown for those coefficients that differ significantly from zero (˙0.1, *0.05, **0.01, ***0.001).

positions (0.31 ± 0.003; Appendix S2: Fig. S3). Hemiepiphytic species reported higher germination probability (0.42 ± 0.003) than non-hemiepiphytic species (0.24 ± 0.003). At both gap and non-gap microsite positions, hemiepiphytic species registered higher germination probability values (NG = 0.39 ± 0.004; G = 0.44 ± 0.004) presenting better performance at gap positions, while germination probability for non-hemiepiphytic species at both microsite positions was low (NG = 0.22 ± 0.003; G = 0.26 ± 0.004; Appendix S2: Fig. S3). Growth form and elevation registered a significant interaction; between 1100 and 1250 m a.s.l we found higher seed germination probability of hemiepiphytic species (0.48 ± 0.007 for both elevations) and at 500 m a.s.l. higher germination probability for non-hemiepiphytic species (0.29 ± 0.006; Appendix S2: Fig. S4).

3.2. Seedling emergence (SEmer)

Emerging fig seedlings experienced significant low probability values (Fig. 2) from a wider variety of environmental factors under random effects of species and site ($R^2m = 0.221$; $R^2c = 0.315$; Appendix S2: Table S3; Fig. 3). Seedling emergence probability was higher in hemiepiphytic species (0.05 ± 0.001; Appendix S2: Fig. S3), in gap microsite positions (0.04 ± 0.001), at greater elevations (higher SEmer probability at 1250 m a.s.l. = 0.07 ± 0.003), and in greater soil temperature (higher SEmer probability at 21.3 °C = 0.072 ± 0.007), soil moisture (higher SEmer probability at 46.8% = 0.086 ± 0.01) and soil pH (higher SEmer probability under 6.1 pH = 0.038 ± 0.003). We also found a significant negative interaction between growth form and elevation; at 1250 m a.s.l. we found higher seedling emergence probability in hemiepiphytic species (0.11 ± 0.004) and at 1100 m a.s.l. higher values for non-hemiepiphytic species (0.02 ± 0.0007; Appendix S2: Fig. S4).

3.3. Seedling establishment (SEstab)

We found very low probability values for *Ficus* seedling establishment (Fig. 2) that was significantly determined by growth form, microsite position and soil pH under site as random effect ($R^2_m = 0.054$, R^2_c = site did not explain enough of the variance; Appendix S2: Table S3; Fig. 3) with hemiepiphytic species, gap microsite positions and higher soil pH (between 6.5 and 6.8) conditions being more favorable for seedling establishment probability (0.004 ± 0.00009, 0.004 ± 0.00008 and 0.005 ± 0.0002, respectively; Appendix S2: Fig. S3).

3.4. Seedling recruitment (SRec)

Seedling recruitment showed less data variation compared to other

ERSs (Fig. 2). The very low probability observed in this stage was mainly due to the absence of suitable microsites for successful seedling recruitment ($R^2_m = 0.161$, $R^2_c = 0.197$; Appendix S2: Table S3; Fig. 3). At this stage, we did not find significant environmental factors driving seedling recruitment.

4. Discussion

The natural regeneration of woody plant communities depends on suitable environmental conditions for seed germination and seedling growth to take place in a physiologically efficient manner. Sites with transient stress conditions typically induce physiological dysfunctionalities that can drastically inhibit growth during regeneration leading to seed or seedling mortality (Kozlowski and Pallardy, 1997). In plants, abiotic factors and the interaction between them as well as inherent biotic limitations can restrict the passage from one ERS to another (Baskin and Baskin, 2014; Kozlowski and Pallardy, 1997). In this study, we show that microclimatic conditions (canopy openness, soil temperature, soil moisture and soil pH) significantly influenced the regeneration of our study species, but the influence depended on each ERS. Recruitment limitation became progressively higher as the plant species moved forward from one ERS to the next and environmental filters were most influential during the seedling emergence stage, creating a niche bottleneck when transitioning from an emerging seedling to become an established seedling (Fig. 3). Here, using an empirical seed addition experiment (Muller-Landau et al., 2002), we show that *Ficus* early regeneration was significantly limited by the lack of adequate microsites rather than due to lack of seeds.

Limited recruitment opportunities that hinder the successful transition through each ERS can explain *Ficus* rarity as well as co-existence and guide specific management goals, which in turn are driven by several aspects such as site limitations. The microsite conditions that best explained the limitation of the ERS in the eight *Ficus* species studied here were light availability, soil humidity, soil temperature and soil pH; regeneration was less limited in gaps between 30 and 55% openness, soil temperature around 24 °C, soil humidity around 48% and soil pH around 6.8. Microsites with good moisture retention can facilitate seed germination and early seedling survival (Laman, 1995; Ramirez W., 1976; Swagel et al., 1997). Indeed, laboratory studies on the seed germination, seedling growth and survival of *Ficus* species have shown that high light (Chen et al., 2013; De Figueiredo et al., 1995; Hao et al., 2013), neutral soil pH (Banack et al., 2002; Lin et al., 2008) and temperatures ranging from 21 to 27 °C (Chaves et al., 2007; Ji et al., 2018) increase the success of the early regeneration process. Our result is consistent with the general idea that environmental variability affects the transition in ERS (Clark et al., 1999).

Our data also showed that elevation was not a determining factor for all four ERS of *Ficus* species, but was influential only for seedling emergence; an increase in elevation positively influenced seedling emergence. However, we found a significant interaction between growth form and elevation during seed germination and seedling emergence; as elevation increases, non-hemiepiphyte species present lower seed germination and seedling emergence. In the case of *Ficus*, Segar et al. (2017) found that genetic flow of *Ficus arfakensis* and *F. hahliana* might be driven by environmental limitations along an altitudinal gradient in forests of Papua New Guinea. Thus, elevation and associated microclimatic conditions can be considered as important drivers of *Ficus* speciation across tropical lowland and highland sites. In subtropical forests, changes in microenvironmental conditions along elevation are known to be associated with changes in species composition (Lu et al., 2015; Tang and Ohsawa, 1997). Microenvironmental heterogeneity observed along altitudinal gradients is more important as a driving force for species co-existence during the seed-to-seedling transition, while in later adult life history stages macro disturbance events such as catastrophic landslides can strongly affect the coexistence (Masaki et al., 2007).

Although the effects of elevation on plant recruitment in different types of forests is commonly assessed on larger, adult size classes (Benavides et al., 2016; Giménez-Benavides et al., 2008, 2007; Gworek et al., 2007; Martini et al., 2020), very few studies report the effect on the stages that composes the early regeneration process. Our study is one of the few that has provided empirical data on the *Ficus* regeneration process under field conditions using contrasting set of hemiepiphytic and non-hemiepiphytic species. It elucidates the critical role that environmental filters play in determining recruitment by specifying which factors during which transitional stages lead to the broad mortality events common during early regeneration. Understanding the mechanisms that govern limitations within plant regeneration processes may explain why many species fail to change their ranges at high elevations or latitudes, how forests will respond to climate change and how future forests will be composed (Harsch et al., 2009; Kroiss and HilleRisLambers, 2015).

Among the environmental factors here assessed, we found that soil moisture was not a significantly determining factor for the early regeneration process, but light availability was a significant driver for the three first ERS; in areas with low light availability will result in lower probabilities of seed germination, seedling emergence and seedling establishment. Our results coincide with Hao et al. (2010) findings. They identified that *Ficus* presents characteristics of high light demanding species such as high plasticity under irradiation and high rates of photosynthetic assimilation. Fu et al. (2008) found that light is an essential factor for seed germination of *F. benjamina* L. var. *nuda*, which can be a strategy for long-term adaptation in tropical rain forest habitats.

Plant regeneration is governed not only by environmental conditions but also by the life history strategy of plants. Plants come in a wide variety of sizes and shapes, and can be classified into growth forms, that allow them to adjust to certain environmental conditions becoming an important factor that underpins the ecosystem structure and diversity (Rowe and Speck, 2005). The experiments presented here were conducted on the forest floor and hence, we expected that non-hemiepiphytic species would perform better than hemiepiphytic as they would be in their preferred habitat. However, we found that non-hemiepiphytic were more limited than hemiepiphytic species. In our study, the hemiepiphytic versus non-hemiepiphytic growth form of the eight *Ficus* species did not determine seedling recruitment, but significantly governed seed germination, seedling emergence and seedling establishment stages, being the non-hemiepiphytic species the less favored to move forward from one stage to another.

Unique evolutionary characteristics and clear differences in the functional traits have been identified in the group of hemiepiphytic species in the genus *Ficus*. Hao (2010) determined that the ability to conserve water in hemiepiphytic species is crucial to survive in drought conditions that can be important under canopy conditions. In germination chamber experiments conducted by Chen et al. (2021), hemiepiphytic species were more resilient to drought conditions and germination peaked at 25/15 °C, day and night temperature. This is consistent with the temperatures in the low elevation germination observed in our study. However, seedling recruitment observed in the chamber germination experiments were much greater (27.15% ± 2.38; Chen et al., 2021) compared to our study (0.06% ± 0.1), indicating greater limitations on the ERS under natural field conditions. Other studies have found a strong relationship between growth form and seed size (Gross, 1984), seed mass, dispersal mode (Jurado et al., 1991), geographic range (Akwood et al., 1993) with significant effects on plant establishment (Gross, 1984). Ours is the first to demonstrate that the hemiepiphytic versus non-hemiepiphytic life forms show differential effects on the seed-to-seedling regeneration stages under field conditions.

The relative contribution between ERSs can be used to identify which is the most important stage that contributes to an individual fitness (Eriksson and Ehrlén, 2008). The regeneration stages of a species allow us to understand the process of evolutionary divergence in plants during the most critical life history stage and subsequently the influence on the populations and community dynamics, which, in turn, facilitate management strategies formulation for plant community conservation (Grubb, 1977; Larson et al., 2015). Greater proportion of plant mortality occurs during the seed-juvenile transition stages, which determine the future populations of a species or a plant community (Grubb, 1977; Larson et al., 2015). From all four early regeneration stages, seed germination was the least limiting and seedling recruitment the most limiting stage. While seed germination probability was significantly governed by two factors and one interaction, seedling establishment by three factors and seedling recruitment did not present a determining factor, seedling emergence was driven by four factors and one interaction. Therefore, contrary to expectations, seedling emergence was the most sensitive stage to the variation in environmental filters, due to the greater number of factors (intrinsic: growth form and extrinsic: environmental factors) that affect this stage, significantly blocking the transition from seedling emergence to seedling establishment.

The final result of a regeneration process determines the success or failure of the regeneration of an entire population (Pausas et al., 2009). If one of the ERSs fail, it becomes a significant ecological bottleneck. Several studies in plant ecology have reported that early plant regeneration is decisive for the final recruitment outcome, since it is in this process where the greatest risk of mortality occurs due to lack of resources available for survival (Baskin and Baskin, 2014; Clark et al., 1998; Kitajima and Fenner, 2000; Kozlowski and Pallardy, 1997). However, there are only a few studies that show which seed-seedling stages are critical bottleneck for the successful regeneration process (Larson et al., 2015). In the case of *Ficus* species, they are considered to have limited recruitment opportunities because of their stringent microsite requirements (Harrison, 2005a, 2003) and despite high seed production, this filter is not totally overcome as stated for other species (Holl et al., 2000).

Our findings could be beneficial for understanding the ecophysiology and subsequent population assembly of hemiepiphytic and non-hemiepiphytic species of the genus *Ficus*. It seems that hemiepiphytic species do not necessarily depend on a host tree to establish, since their ecological and evolutionary attributes would allow them to survive if lack of host trees forces the species to grow on the forest floor as long as they find suitable conditions for seedling recruitment. However, deeper evaluation of the ERSs in the canopy is required. Other studies have shown that microsite conditions, including animal predation, pathogen infection and plant litter, are the main constraints for survival and successful plant recruitment in subtropical forests of southern China (Lu et al., 2015; Luo et al., 2013; Martini and Goodale, 2020; Martini et al., 2020, 2021). The subtropical forests of southern China, where this study was conducted, have faced intense land use transformations due to monoculture rubber and eucalyptus plantations (Ashton and Zhu, 2020). This has led to diminished forest habitat and increased forest fragmentation and biodiversity loss (Zhu et al., 2015, 2006), which could significantly alter the regenerative capacity in forested systems (Zhu, 2017). Hence, further studies of other constituent species of these forested communities to determine the factors that limit recruitment are called for. The approach of forest management plans for reintroduction of local biodiversity and construction of biological corridors that connect forest fragments will surely improve the quality of microsites available for the early regeneration process from seed arrival, seed germination, seedling establishment to seedling recruitment of species with high biological and ecological importance that will contribute to reassemble resilient forests able to adapt to climate change and to provide resources for humanity.

5. Conclusions

This study demonstrated that niche-based seedling recruitment limitations imposed by multiple environmental filters affect *Ficus* early regeneration stages, and likely determine community assembly in time and space. The process of early regeneration in *Ficus* species in our subtropical landscape was highly limited, with light and soil condition strongly influencing early regeneration stages. The limitation peaked when transitioning from an emerged seedling to an established seedling and non-hemiepiphytic species were more limited. Our results corroborate that *Ficus* is not successfully recruited and found in low densities, but for the first time we show that the limitation in recruitment is due to a blockage during seedling emergence and the seedling establishment, since it is here where *Ficus* seedlings face a greater number of environmental factors and interactions that makes the passage from one stage to another difficult. We have identified that this blockage is due to the limited availability of adequate microsites or habitats for the species survival, but not due to the lack of seeds. We consider that the partition of the plant regeneration process in different stages according to morphological or physiological changes is important to accurately identify the bottlenecks that have significant implications for the final plant recruitment in both restoration areas and natural remnant areas. These findings provide an important basis for the development of effective management and restoration strategies when producing seedlings or introducing seeds or seedlings of *Ficus* species, which are of high ecological, agricultural and industrial importance.

CRediT authorship contribution statement

Diana Castillo-Díaz: Conceptualization, Methodology, Investigation, Formal analysis, Writing - original draft. **Huayang Chen:** Methodology, Formal analysis, Writing - review & editing. **Rhett D. Harrison:** Methodology, Writing - review & editing. **Bin Wen:** Writing - review & editing. **Uromi Manage Goodale:** Conceptualization, Methodology, Supervision, Funding acquisition, Writing - review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2021.119536. The research data to this manuscript available at: https://figshare.com/articles/dataset/Castillo-Diaz_et_al_2021_Forest_Ecology_and_Management_xlsx/14999976.

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