

## GAMETOPHYTE ECOLOGY AND DEMOGRAPHY OF EPIPHYTIC AND TERRESTRIAL TROPICAL FERNS<sup>1</sup>

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Factors that influence the distribution of ferns are poorly understood and likely reflect the ecology of both the sporophyte and the gametophyte generation. Little study has been done on the ecology of the gametophyte generation, especially in regard to tropical species. The goal of this study was to examine demography and the influence of light and disturbance on the distribution of the gametophytes of several tropical epiphytic, hemiepiphytic, and terrestrial fern species. Through a series of observational and experimental studies, we found that increased terrestrial gametophyte density and richness were related to both increased light and disturbance. By contrast, increased light had no influence, and increased disturbance negatively affected epiphytic density. Over a 25-mo demographic study, epiphytic and hemiepiphytic species had significantly greater longevities and lower recruitment rates than terrestrial species. Such unique strategies may have evolved in response to different disturbance regimens between the two habitats. Terrestrial species encounter and are adapted to more frequent disturbance and have invested in rapid gametophyte growth and recruitment. Epiphytic species may be more influenced by bryophyte competition, and in habitats of relatively low disturbance, they have invested in greater size and longevities. In such systems, gametophytes are able to survive for years waiting for favorable recruitment conditions.

**Key words:** demography; disturbance; ecology; gametophyte; pteridophytes; tropical ferns.

Though the study of ferns has been fundamental to our understanding of vascular plant biology, even the most basic aspects of fern ecology have only begun to be examined. Because ferns have both independent gametophytes and sporophytes, ferns can reveal important aspects of the ecology of organisms with two free-living and fundamentally different generations. With the retention of the independent gametophyte, ferns also hold tremendous potential to teach us about the evolutionary ecology of early vascular plants.

The paucity of ecological information on the ferns is surprising given that they play important roles at the ecosystem level in both temperate and tropical forests. For example, ferns have been shown to control the regeneration potential of forests throughout the world (George and Bazzaz, 1999; Coomes et al., 2005). In tropical forests, basket-forming ferns can harbor more arthropod diversity in a single individual than occurs in the entire canopy of the fern's host tree (Ellwood and Foster, 2004). Ferns can also be critical players in ecosystem establishment (Russell and Vitousek, 1997). While we have some knowledge of the role of ferns in forests, our knowledge of the organismal ecology of ferns is phenomenally limited. This is especially true of the gametophyte generation where

there is not a single published report on the factors that control the distribution and survival of tropical species. Not surprisingly, fern gametophyte ecology has historically been viewed with a temperate slant, leaving science with a decidedly biased and limited view of this stage of the life cycle. The goal of this paper is to correct some of these biases through a detailed examination of the autecology of tropical gametophytes.

Much of what we know of gametophyte ecology is often anecdotal (e.g., Holttum, 1938), derived from studies and observations made from sporophytes, or comes from comments obscured in floristic inventories (e.g., Mickel and Beitel, 1988). Modern studies have attempted to describe both the patterns of fern sporophyte diversity and the causal relations behind such patterns (Tuomisto and Ruokolainen, 1994; Tuomisto and Dalberg, 1996; Tuomisto et al., 1998; Tuomisto and Poulsen, 2000; Jones et al., 2006; Watkins et al., 2006a,b). While these studies have been critical for developing ecological models to better understand the biology of the fern sporophyte, the gametophyte has not been considered as the primary mechanism initially shaping sporophyte distributions. It is critical to remedy such limitations before we can truly begin to understand fern ecology.

What makes the group exceptional is the life cycle that alternates between two *independent* generations: the haploid gametophyte and the diploid sporophyte. The gametophyte is a fundamentally different organism than the sporophyte. It lacks vascular tissue, produces rhizoids instead of true roots, has poorly developed to non-existent cuticles, has little ability for internal water capacitance, and is comparatively small (Raghavan, 1989). Given such differences, it is not surprising that the gametophyte has radically different ecologies from that of the sporophyte. For example, gametophytes can be more widespread than, grow in areas that are uninhabitable to (Farrar, 1967; Peck, 1980; Peck et al., 1990), and have a greater degree of stress tolerance than sporophytes (Sato and Sakai, 1980, 1981; Watkins, 2006).

Every sporophyte population owes its beginnings to the gametophyte generation. Thus, understanding gametophyte

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biology is critical to ultimately understanding sporophyte distributions. Multiple factors clearly act at the level of the gametophyte and studies have demonstrated the importance of disturbance and edaphic factors (Cousens, 1979, 1981, 1988; Cousens et al., 1985, 1988; Greer and McCarthy, 1999), and plasticity (Greer and McCarthy, 1999) on the distribution and survival of temperate gametophytes. Data on tropical fern gametophytes suggest that there may be considerable differences among different functional groups. For example, both gametophyte ontogeny and morphology often vary tremendously among epiphytic and terrestrial species (Atkinson and Stokey, 1964; Nayar and Kaur, 1971). A common observation is that there are apparent fundamental differences in morphology and potentially longevity between the gametophytes of epiphytic and terrestrial species (Dassler and Farrar, 1997, 2001). Epiphytic species often produce gametophytes with diverse morphologies that are frequently capable of asexual reproduction and are theoretically long-lived. Most terrestrial species are thought to produce the textbook short-lived, cordate thallus and have little ability to reproduce asexually (but see Watkins and Farrar, 2005). Few quantitative data have been generated to back up such longevity claims, and we have been unable to find a single paper that describes factors that influence the distribution or demographic characteristics of tropical gametophytes.

The goal of our study was to examine the distribution of fern gametophytes to (1) understand factors that sort species in tropical forests, (2) examine the demography of several tropical epiphytic, hemiepiphytic, and terrestrial species, and (3) quantify purported differences between these different functional groups. We first examined the distribution of epiphytic and terrestrial gametophytes and, based on previous field experience, hypothesized that both increased disturbance and light would result in greater epiphytic and terrestrial gametophyte species richness and density. We then examined the gametophyte demography of five species of different functional groups and hypothesized that the gametophytes of epiphytic and hemiepiphytic species would be significantly longer lived and exhibit less recruitment to the sporophyte phase than terrestrial species.

## MATERIALS AND METHODS

**Study site**—This study was conducted at La Selva Biological Station (Heredia Province) in the Atlantic lowlands of northeastern Costa Rica (10°25.591' N, 084°00.137' W). La Selva is a 1400 ha tropical wet forest having a mean annual rainfall of about 4300 mm, with peaks of precipitation in June–July and November–December and a drier period in March. Mean monthly rainfall nevertheless never falls below 150 mm in any month during the dry season based on long-term meteorological records.

**Gametophyte transects**—The occurrence of gametophytes in nature was examined in 425 plots (25 × 25 cm) placed along 50 randomly chosen terrestrial 50 m transects and in 425 (25 × 25 cm) canopy plots placed in nine canopy trees along 3–5 m long transects within the inner canopy. Both terrestrial transects and canopy trees were sampled from primary forests on similar soil types in the “old La Selva” section of the biological station. The total number of gametophytes was recorded, and each quadrat was coded for level of surface (i.e., leaf litter) and soil depth (i.e., varying degrees of surface scarification) disturbance. Categories were 0 = undisturbed (<5 cm<sup>2</sup> soil surface exposed and no surface scarification); 1 = low disturbance (i.e., >5 cm<sup>2</sup> soil surface exposure and no surface scarification); 2 = medium disturbance (>5 cm<sup>2</sup> soil surface exposure with surface scarification); 3 = high disturbance (>5 cm<sup>2</sup> soil surface exposure and soil completely turned over). Additionally,

each quadrat with a disturbance rating of level 1 and above was coded for the type of damage when possible. Light environment was assessed with a digital hemispherical photograph taken with a Nikon Coolpix 950 digital camera (Melville, New York, USA) with a fisheye lens attachment and analyzed using Gap Light Analyzer software (Frazer et al., 1999) to estimate the percentage of total light transmittance. Photos were taken 25 cm above each quadrat. For determining the influence of light environment on density, both gametophyte number and percentage canopy transmittance were log transformed and analyzed by regression analysis. We used ANOVA to determine the influence of level of disturbance on gametophyte density. Unless otherwise stated, all analyses were performed with the computer program JMP version 5.01 (SAS Institute, 2005).

**Disturbance plots**—The influence of disturbance and light on terrestrial fern establishment was studied in 20 disturbance plots that were established and monitored for gametophyte density at 4 and 6 mo post establishment. All plots were established on the same soil type in primary forest, with 10 plots placed in low-light understory habitats (PPFD: 5–14 μmol·m<sup>-2</sup>·s<sup>-1</sup>) and 10 placed in high-light canopy gaps (PPFD: 625–784 μmol·m<sup>-2</sup>·s<sup>-1</sup>) of similar age. Each plot measured 1 m<sup>2</sup> and was divided into four 0.5 × 0.5 m subplots of increasing disturbance similar in degree to those found in nature. The undisturbed treatment subplot acted as the control. For the low disturbance level, we removed all leaf litter with no mechanical surficial scarification to the soil. For the medium disturbance level, we disturbed the first 5 cm of soil with a metal sand rake. For the high disturbance level, we physically turned over the soil with a shovel to a depth of approximately 20 cm. Gametophyte density and richness were recorded in the center 25 cm<sup>2</sup> area of each subplot (disturbance level). Litter-fall was removed from the disturbed subplots weekly, and after 4 and 6 mo, all plots were assessed for density (and when possible, richness of gametophytes). Canopy openness (a proxy for light environment) was determined with digital photography as discussed. Gametophyte were grouped into morphotypes that may represent multiple species. Morphotypes were assigned based on morphological characters identifiable by a 10× or 20× hand lens. Characters included trichome presence and type, rhizoid color, gametophyte shape, and the presence and morphology of gemmae. Identification of fern species from gametophytic characters should be taken as a conservative estimate of actual species richness. A full factorial ANOVA was used to determine the effects of light and disturbance intensity on gametophyte density and diversity.

**Demographic study**—In June 2003, gametophytes from three populations of five species were located and marked in the field. Species were selected to represent typical examples of either epiphytic, hemiepiphytic, or terrestrial species at the site. The two epiphytic species included in the study were *Campyloneurum brevifolium* (Lodd. ex Link) Link and *Vittaria lineata* (L.) Sm. Both species are common and occupy similar habitats being found in the inner-canopy and in high-light understory sites. The hemiepiphytic *Lomariopsis vestita* E. Fmyn. is abundant and occurs in the understory of both primary and secondary forests throughout La Selva. *Danaea wendlandii* Rchb. f. is a terrestrial species typical of more stable understory habitats of primary forests; whereas *Pityrogramma tartarea* (Cav.) Maxon is an abundant species that is often found in disturbed sites such as trail and road sides as well as the root-balls of recently fallen trees. Marked individuals were censused monthly for the next 15 mo with a final census at 25 mo. No data were recoded during the months 5–7. At each census, individuals were recorded as present, dead, or missing, or as recruits into the sporophyte generation. When possible, individuals were coded for cause of mortality.

In the case of terrestrial species, gametophytes were marked with a numbered aluminum nail, whereas the epiphytic species were either marked with a nail or with a numbered tag attached to the substrate with copper wire. It was not possible in all cases to determine precisely the initial age of marked gametophytes. Therefore, individuals were chosen according to their initial size. Initial sizes were held constant within a species but differed among the species. Longevity was calculated as the time between the initial mark (treated as birth) and death of each gametophyte. A major flood event occurred in month 11 of the study. All individuals were sampled 3 d before the flood (for the regularly scheduled month 11 survey) and then 3 d after the flood to serve as an extra survey to determine the influence of flooding. The next sample period took place on the next corresponding survey day and was recorded as the month 12 survey. This allowed for more precise determination of mortality due to flooding rather than categorizing these individuals in the unknown category.

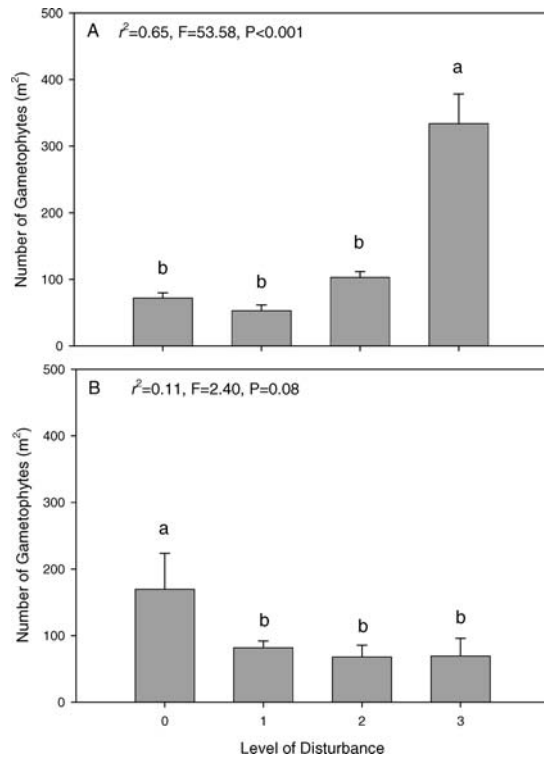


Fig. 1. Mean number of gametophytes and their relation to natural disturbance in both (A) terrestrial habitats and (B) canopy habitats at La Selva Biological Station (Heredia Province) in the Atlantic lowlands of northeastern Costa Rica. Categories are 0 = undisturbed (<5 cm<sup>2</sup> soil surface exposed and no surface scarification); 1 = low disturbance (i.e., >5 cm<sup>2</sup> soil surface exposure and no surface scarification); 2 = medium disturbance (>5 cm<sup>2</sup> soil surface exposure with surface scarification); 3 = high disturbance (>5 cm<sup>2</sup> soil surface exposure and soil completely turned over). Error bars represent standard errors; differences among levels were calculated by post hoc Tukey tests; levels sharing the same letter are not significantly different.

**Gametophyte survival analysis**—Throughout this paper, we use the term recruitment in a restrictive sense to specifically refer to the successful passage of an individual from the gametophyte stage into the sporophyte stage, i.e., the production of juvenile sporophytes. Recruitment into a population typically refers to an individual that has become established and has successfully matured. We view the gametophyte’s production of the sporophyte as successful maturation of the gametophyte, and thus the restricted use of the term recruitment is appropriate, albeit used restrictively. As with many demographic studies, individuals can be lost from the study by different avenues. Such absent samples were coded as right-censored data points (Hollander and Wolf, 1999). In this study, only those individuals that recruited and those still alive at the end of the experiment (25 mo) were recorded as censors. As described later, certain species exhibit little recruitment but have extremely long-lived gametophytes, whereas others exhibit the opposite pattern. Given such radical differences among the species, we also plotted the cumulative proportion of individuals that recruited at each time interval (i.e., the proportion of gametophytes that produced a juvenile sporophyte).

Gametophyte survival functions were estimated using nonparametric Kaplan–Meier product-limit survival functions (Collet, 2003). These analyses were also used to estimate a mean life span for each species. Log-rank  $\chi^2$  statistics were computed to test for homogeneity of the survival functions for all species. Weibull distributions were used to model survivorship functions and to calculate the parameters  $\alpha$  and  $\beta$ . The scale parameter  $\alpha$  is a measure of the degree of hazard for a species, whereas the shape parameter  $\beta$  determines the degree of change in the hazard function over time. Large values of  $\alpha$  correspond to low hazard levels (i.e., greater survivorship) where low values equate to rapidly decaying survivorship. Large values of  $\beta$  (i.e., >1) correspond

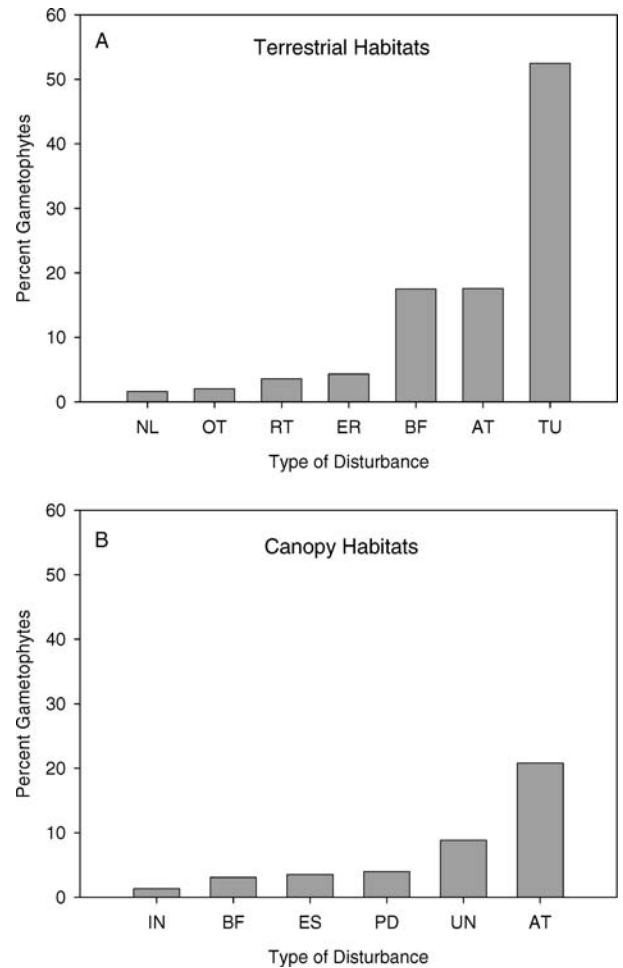


Fig. 2. The percentage of fern gametophytes as influenced by specific naturally occurring types of disturbance at La Selva Biological Station (Heredia Province) in northeastern Costa Rica. (A) In terrestrial habitats (NL: no leaf litter, OT: old tip-up mound, RT: rotting tree/wood, ER: erosion, BF: branch fall, AT: animal trail, TU: recent tip-up mound). (B) In canopy habitats (IN: insect damage, BF: branch fall, ES: epi-slide, PD: physical damage, UN: unknown, AT: animal trail).

to an increasing hazard rate that affects older individuals over younger individuals. With a  $\beta < 1$ , younger individuals are more likely to die within the experimental period.

RESULTS

**Transects**—A combined total of 2096 gametophytes was counted with 329 recorded from canopy, 538 from low-trunk, and 1229 from terrestrial habitats. The level of disturbance significantly affected the number of gametophytes in terrestrial habitats (Fig. 1a,  $r^2 = 0.65$ ,  $F_{3,1225} = 53.58$ ,  $P < 0.001$ ) with greater numbers of gametophytes found in more disturbed habitats. Less than 1% of terrestrial gametophytes were found in areas without disturbance. The opposite trend was apparent in canopy habitats where the level of disturbance had less influence on gametophyte number (Fig. 1b,  $r^2 = 0.11$ ,  $F_{3,235} = 2.40$ ,  $P = 0.08$ ) and gametophytes occurred in less disturbed

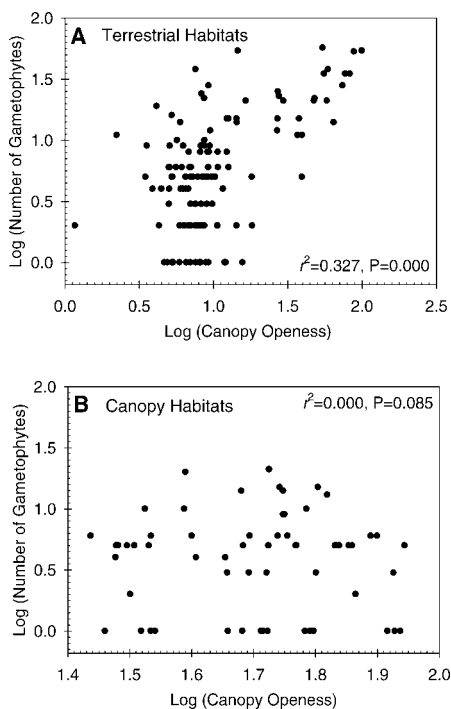


Fig. 3. The relationship between log canopy openness (a proxy for light intensity) and log gametophyte density for (A) 425 terrestrial plots and (B) 425 canopy plots at La Selva Biological Station (Heredia Province) in northeastern Costa Rica. Canopy openness was determined by digital hemispherical photographs analyzed with Gap Light Analyzer software (Frazer et al., 1999).

habitats (58% of canopy gametophytes were found in areas with no disturbance).

In terrestrial transects, seven causes of disturbance were identified: leaf litter removed, new and old root tip-ups from fallen trees, rotten logs, erosion, branch falls, and animal causes (Fig. 2a). Six causes of disturbance were identified in canopy habitat: insect, branch falls, epi-slides, physical damage of unknown origin, animal, and unknown causes (Fig. 2b). Identification of causes in the low-trunk habitat was difficult; thus this habitat was excluded from all analyses. In the case of terrestrial species, recent root tip-ups harbored the greatest number of gametophytes (>50%). The disturbance category with the greatest percentage of gametophytes in canopy habitats was animal disturbance with approximately 20%. In addition to disturbance, canopy openness (as a surrogate for light level) had a positive effect on the number of terrestrial gametophytes (Fig. 3a,  $r^2 = 0.327$ ,  $P = <0.0001$ ), but had little influence on canopy gametophyte density (Fig. 3b,  $r^2 = 0.0001$ ,  $P = <0.085$ ).

**Disturbance plots**—A total of 1247 gametophytes from 16 morphotypes were counted in the experimentally disturbed plots with six non-unique morphotypes found in the low light treatment. There were a total of 16 types, of which 10 were unique, in the high light treatments. Increasing light and disturbance and the interaction of light and disturbance significantly and positively affected gametophyte density among the plots (Fig. 4, Table 1). Likewise, morphotype richness was significantly influenced by both light and disturbance, but there was no significant interaction (Table

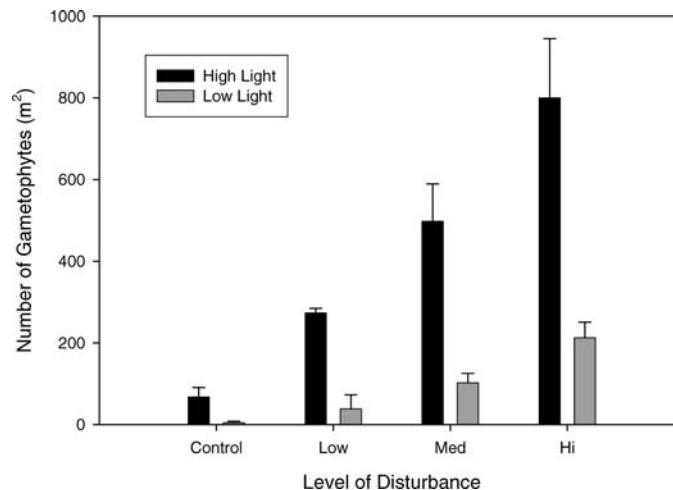


Fig. 4. Gametophyte densities as influenced by light and disturbance in experimentally created plots at La Selva Biological Station (Heredia Province) in northeastern Costa Rica. Disturbance treatments were designed to simulate natural disturbance seen in the field and that reported in Fig. 1. All plots were established on the same soil type in primary forest, with 10 plots placed in low-light understory habitats (PPFD: 5–14  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ) and 10 placed in high-light canopy gaps (PPFD: 625–784  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ) of similar age. The undisturbed treatment subplot acted as the control. For the low disturbance level, all leaf litter was removed with no mechanical surficial scarification to the soil. The medium disturbance level was raked with a metal sand rake to disturb the first 5 cm of soil. The high disturbance level was physically turned over with a shovel to a depth of approximately 20 cm. Error bars represent standard errors.

1). Disturbance plots were not created in canopy habitats for reasons noted in the Discussion.

**Demography**—All combined, 809 gametophytes from five species were marked and followed throughout the demographic study. A total of 263 gametophytes was marked from the understory terrestrial species *Danaea wendlandii*. All three populations of this species were recorded in the understory of primary forests from sites that were at least 50 m from trail sides. We marked 275 gametophytes of *Pityrogramma ebenea*, an abundant species often found in full to partial sun in disturbed sites such as road and trail sides. All populations of *P. tartarea* were recorded from disturbed sites within the forests or in open areas away from trail sides. Sixty-seven gametophytes of the understory hemiepiphyte *Lomariopsis*

TABLE 1. Relationship of gametophyte density and richness with three levels of experimental disturbance and two light levels at La Selva Biological Station (Heredia Province) in the Atlantic lowlands of northeastern Costa Rica. Data were analyzed by a  $2 \times 4$  full factorial ANOVA.

Source	df	F	P > F
<b>Gametophyte density</b>			
Light	1	52.643	0.000
Disturbance	3	18.567	0.000
Light $\times$ disturbance	3	6.152	0.001
<b>Number of species</b>			
Light	1	46.522	0.000
Disturbance	3	6.662	0.000
Light $\times$ disturbance	3	0.364	0.779

TABLE 2. Demographic and survival analyses for the gametophytes of five fern species at La Selva Biological Station (Heredia Province) in northeastern Costa Rica using the Wilcoxon test to compare survival distribution functions for different species. Three populations of each species were followed for 25 mo. *Danaea wendlandii* is a common terrestrial species in the understory of primary forests, *Pityrogramma ebenea* is an abundant species often found in full to partial sun in disturbed sites such as road and trail sides. All populations of this species were recorded from disturbed sites within the forests or in open areas away from trail sides. The understory hemiepiphyte *Lomariopsis vestita* were marked from small diameter trees that all occurred in primary forests. Two canopy epiphytes were also marked: the high-light *Vittaria lineata*, and the medium-light *Campyloneurum brevifolium*.

Species	Number of gametophytes			Survival analysis			
	Dead	Recruited or alive at end of study (censored)	Total	Mean longevity (mo)	Std	$\chi^2$	$P > \chi^2$
<i>Campyloneurum brevifolium</i>	19	87	106	22.9	0.57	386.2	<0.0001
<i>Danaea wendlandii</i>	168	95	263	12.3	0.56		
<i>Lomariopsis vestita</i>	22	45	67	20.8	0.82		
<i>Pityrogramma tartarea</i>	165	110	275	4.1	0.28		
<i>Vittaria lineata</i>	40	58	98	16.6	1.08		

*vestita* were marked from small diameter trees in primary forests. Two canopy epiphytes were also marked: 98 from the high-light epiphyte *Vittaria lineata* and 106 from the high- to medium-light understory epiphyte *Campyloneurum brevifolium*.

Survival distribution functions varied significantly among species for the entire survey period (Table 2, log-rank  $\chi^2 = 386.2$ ,  $df = 4$ ,  $P < 0.0001$ ). *Campyloneurum brevifolium* had the highest mean longevity (22.9 mo), five times that of *Pityrogramma tartarea* (4.1 mo) (Figs. 5a, 6a). When combined, the epiphytic species, *C. brevifolium*, *Lomariopsis vestita*, and *Vittaria lineata* had higher mean longevities than the terrestrial species (log-rank  $\chi^2 = 212.3$ ,  $df = 1$ ,  $P < 0.0001$ ). In all cases,  $\beta > 1$ , indicating an increasing hazard rate and suggesting that older individuals were more likely to die than younger individuals over the study period. Percentage recruitment varied among the species, with *C. brevifolium* < *V. lineata* < *D. wendlandii* < *L. vestita* ~ *P. tartarea*.

The cumulative proportion of gametophytes recruited varied for all species over the sampling time of the study (Fig. 6b). Initial recruitment was highest for both terrestrial species. More than 30% of *P. tartarea* gametophytes had recruited between plot establishment and the first census, no additional individuals were recruited beyond month 8. Initial recruitment was lower for *D. wendlandii*, but increased throughout the study. Recruitment was lowest for *V. lineata* and *C. brevifolium* with essentially no recruitment after the third census through month 25 (Fig. 6b). The percentage of gametophytes still alive at the end of the study also varied from 0% in *P. tartarea* to just over 70% in *C. brevifolium* (Fig. 5b).

Seven causes of mortality, including an unknown category, were surveyed in the field. Catastrophic habitat failure occurred in habitats where over 95% of the individuals were lost. This happened when entire trees fell in the case of epiphytes or when hillsides with some terrestrial species collapsed. Flooding also resulted in catastrophic failure, but was separated as a unique disturbance type because we were able to directly assess its influence. Minor erosion resulted in the loss of some individuals as did another massive flood in month 8 of the study. Fungal attack, herbivory, and physical damage (e.g., from a branch or rock fall that physically removed individuals from the population) were also identifiable causes of mortality. The unknown category consisted of a contribution from all of these plus other unidentifiable disturbances. Most mortality was attributable to unknown causes, such as an individual

simply missing from the population without any sign of disturbance.

## DISCUSSION

**Gametophyte distributions**—The present study clearly demonstrates the importance of disturbance for gametophyte establishment of terrestrial tropical fern species. The majority of the undisturbed sites had no established gametophytes. At the lowest level of naturally occurring disturbance, the maximum number of terrestrial gametophytes found was three, and this from only four plots. In our manipulations of disturbance, even the minor disturbance of leaf litter removal stimulated some gametophyte establishment, providing further evidence for the important role soil disturbance plays in gametophyte establishment and increasing species richness.

There are several likely explanations for these observed patterns. Disturbance that physically turns the soil not only produces an exposed and competition-free habitat, it can also expose the underlying spore bank. This exposure provides additional propagules that may further contribute to density and richness. Subtle changes in soil nutrient composition and structure may also contribute to the disturbance–establishment relationship.

Disturbance has been indirectly linked to gametophyte establishment in studies on temperate species. For example, disturbance may create nutritional and edaphic “safe sites” that are important for gametophyte establishment of both *Woodwardia areolata* (Cousens et al., 1988) and *Blechnum spicant* (Cousens, 1981). Apart from disturbance, gender expression has been shown to influence gametophyte distributions in some species (Klekowski, 1969; Crist and Farrar, 1983) but not in others (Holbrook-Walker and Lloyd, 1973; Greer and McCarthy, 1999). These studies, combined with the results of our work, demonstrate that while disturbance is critical, gametophyte distributions are likely controlled by a combination of factors.

The nature of disturbed habitats can create positive feedback for species that prefer disturbed sites. By their very nature, such sites are often unstable and result in increased mortality due to continued habitat erosion. For example, *Pityrogramma tartarea* is perhaps the most common species of disturbed habitats at La Selva. It frequently grows on the vertical sides of trail cuts and root tip-ups from fallen trees. The populations examined in this paper had the greatest proportion and fastest rates of

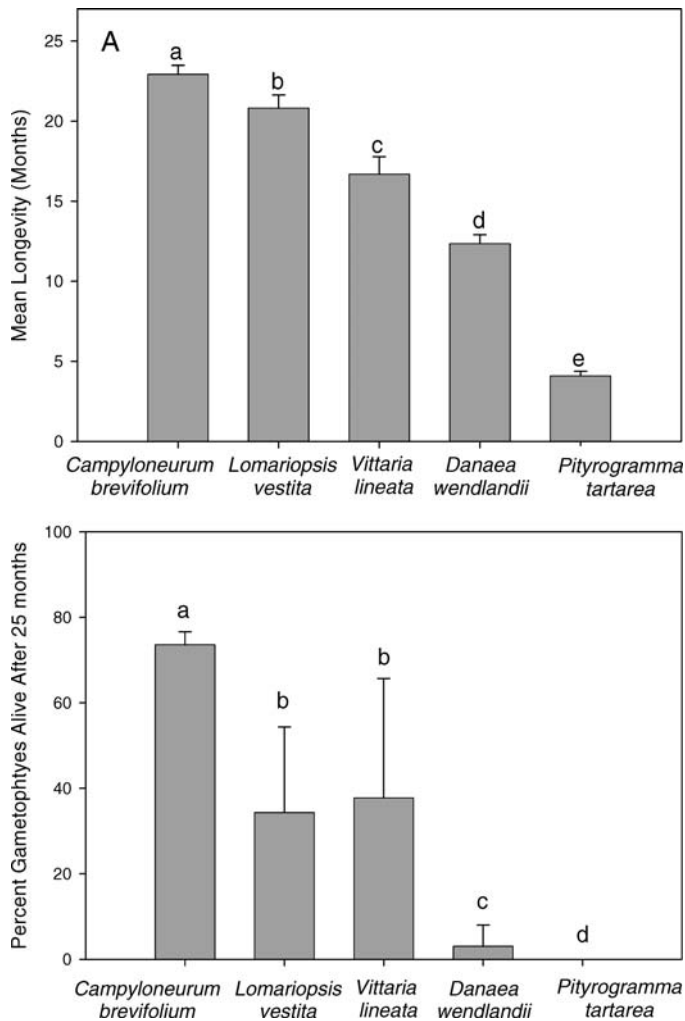


Fig. 5. (A) Mean longevity (months) and (B) and percentage gametophytes still alive and unrecruited for the 25 mo of the study at La Selva Biological Station (Heredia Province) in northeastern Costa Rica. *Campyloneurum brevifolium* and *Vittaria lineata* are epiphytes that commonly occur in the inner-canopy and in high-light understory habitats. *Lomariopsis vestita* is an abundant hemiepiphyte that occurs in the understory of both primary and secondary forests throughout the study site. *Danaea wendlandii* is a terrestrial species typical of more stable understory habitats of primary forests, whereas *Pityrogramma tartarea* is an abundant species that is often found in disturbed sites such as trail and road sides and on the root balls of recently fallen trees. Error bars represent standard errors; levels sharing the same letter are not significantly different.

recruitment. However, continued habitat degradation (by erosion) from extensive wet season rains resulted in no single recruited plant surviving long enough to produce a fertile frond. Such wholesale loss was not observed in species occurring in more stable habitats in this study.

Fern gametophytes had varying levels of disturbance tolerance. For example, *Danaea wendlandii* is a eusporangiate fern. The eusporangiate ferns produce liverwort-like gametophytes that are several cell layers thick. Individual gametophytes are often large and more resistant to physical damage relative to the single-layered gametophytes produced by leptosporangiate species (J. Watkins, personal observation). Tough gametophytes that occur in sites with minor disturbance

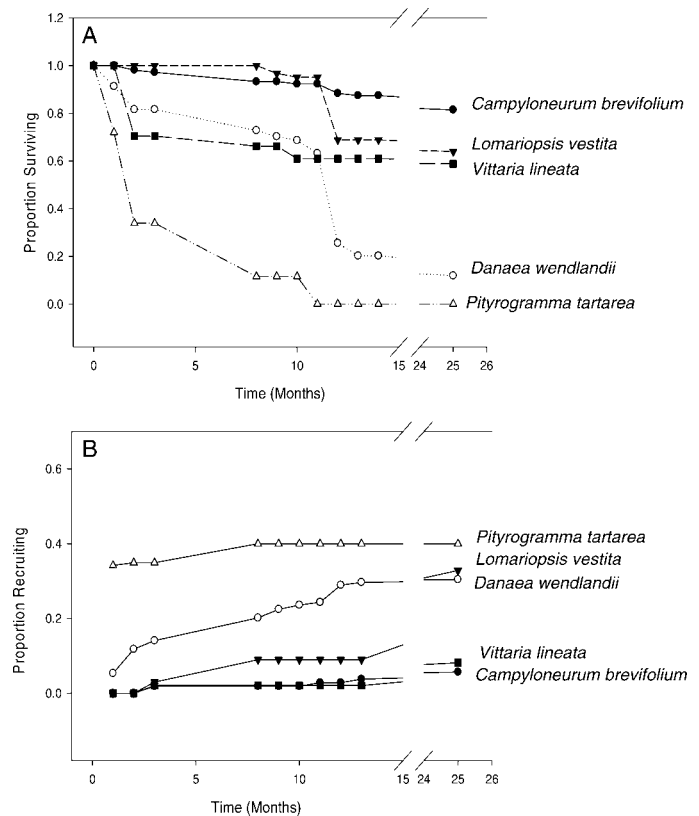


Fig. 6. (A) Kaplan-Meier survivorship curves (B) and proportion recruiting (i.e., proportion of gametophytes producing juvenile sporophytes) of the gametophyte of five species over the 25-mo study period at La Selva Biological Station (Heredia Province) in northeastern Costa Rica. No data were collected during months 4–7 and 15–24. Open symbols indicate terrestrial, whereas closed symbols represent epiphytic and hemiepiphytic species. Species are described in the caption for Fig. 5.

may confer longevity. Indeed, the gametophytes of *D. wendlandii* had three times the mean longevity and significantly less recruitment than those of *P. tartarea*. Two populations of *D. wendlandii* fell in the flood zone and flooding resulted in lower mean longevities in this study.

There were surprising differences between epiphytic and terrestrial species in their response to disturbance. Epiphytic species had significantly less tolerance relative to terrestrial species. Epiphytic habitats are also subject to catastrophic disturbances, but these events appear to be relatively rare. The epiphytic habitats tended to be more stable when compared to terrestrial habitats in this forest. One related emergent difference between species occurring in these two habitats was the percentage of gametophytes that survived but did not recruit. Over 70% of the gametophytes of *C. brevifolium* and over 50% of both *V. lineata* and *L. vestita* (all species with epiphytic gametophytes) were alive and unrecruited by month 26. In contrast, less than 5% *Danaea wendlandii* and 0% *Pityrogramma tartarea* were unrecruited in the same time period. Epiphytic species are not necessarily less capable of producing sporophytes. Over time periods beyond those of this study, the production of sporophytes by epiphytic species may be equal to or greater than that of terrestrial species. These data simply illustrate two fundamentally different gametophytic life history strategies that might profitably be compared to r and K

selection models. They do not imply that a given epiphytic or terrestrial species is more successful than the other, except as relative to their different habitats.

**Density and species richness**—When compared to terrestrial density, canopy gametophyte density is more vulnerable to disturbance, with nearly 58% of the individuals occurring in undisturbed sites. Additionally, there was not a detectable relationship between canopy gametophyte density and light environment as was shown for terrestrial density. Light in canopy environments is significantly higher than in terrestrial sites (Cardelús and Chazdon, 2005), and the lack of a density response to light in habitats where light may not be limiting is not surprising. The canopy does experience a significant amount of disturbance, and some have argued that they are more highly disturbed than terrestrial habitats. Disturbance and light seem to have little influence on canopy gametophyte density. When compared to the typical rainforest understory habitat, the canopy is less buffered and has larger temperature and humidity extremes (Cardelús and Chazdon, 2005). It is plausible that microclimate and water availability play larger roles in these habitats relative to terrestrial sites. Such an observation would be in line with reports by Hietz and Briones (1998) who demonstrated that the distribution of fern sporophytes within the canopy was largely a function of species' water relations.

Quantification of gametophyte species richness in the natural transects was abandoned largely because of difficulties with in situ identification. However, there were clear relationships of light and disturbance with the density of terrestrial species, and for this reason, we examined these variables more completely in the terrestrial disturbance experiment. Increases in both light and disturbance individually generated increased species richness in our field experiment. This result indicates that light and disturbance act independently in shaping gametophyte richness. Clearly, specific differences in gametophyte ecology influence densities and richness at a given terrestrial site. However, the nearly complete absence of gametophytes in undisturbed habitats suggests that disturbance may be critical to the majority of terrestrial species, if not all, regardless of life history. Such natural observations combined with experimental manipulations offer strong evidence that light and disturbance both act to structure terrestrial gametophyte density and richness.

Fern gametophytes likely evolved from ancestors with multilayered, long-lived thalli similar to the modern Osmundales. The relatively rapid gametophytic growth and recruitment in many modern terrestrial leptosporangiate ferns is a derived character that may have evolved from selective pressures related to frequent disturbance as occurred with many r-selected species. Release of such pressures could have occurred concurrently with radiation into the epiphytic habitat. Epiphytic species were faced with increased bryophyte competition, but in relatively undisturbed habitats, were free to invest in greater longevity and clonal growth, which are observed in most epiphytic (Atkinson and Stokey, 1964; Farrar, 1990, 1998) and some epipetric species (Watkins and Farrar, 2005).

The lack of disturbance combined with the presence of leaf litter may be the most important limiting factor to terrestrial species establishment because there are few morphological or physiological pathways that allow a species to survive under leaf litter. The mechanisms behind sporophyte distributions remain complicated because they clearly also rely on gametophyte ecology. Are terrestrial sporophytes elements of

disturbance past? It is, as yet, too early to make such sweeping conclusions; however, such questions warrant greater investigations. Future studies should examine additional aspects of gametophyte autecology. Incorporation of studies on stress physiology of individual gametophytes along with the edaphic and microclimatic requirements of different species should greatly aid our understanding of variables that shape the ecology of this magnificent group of plants.

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